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FOOD HABITS OF EPHEMEROPTERANS FROM THREE ALBERTA, CANADA, STREAMS

by

(C) HAL ROBERT HAMILTON

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled ....Food Habits of Ephemeropterans from Three Alberta, Canada, Streams ......

submitted by ....Hal Robert Hamilton....

in partial fulfilment of the requirements for the degree of Master of Science in Zoology.

THIS WORK IS DEDICATED

TO THE MEMORY OF MY FATHER

LLOYD E. HAMILTON

ABSTRACT

Food habits of mayfly nymphs from four sites of three Alberta streams were studied from July 1975 until July 1976. The purpose was to determine differences in food items consumed amongst species, nymphal size classes, seasons, and different type streams. Nymphs obtained from a brown-water muskeg stream, a foothills stream, and a springfed stream with an agricultural watershed were analyzed to determine the relative importance of detritus versus algal material as food resources.

In terms of volume, detritus was the dominant food item ingested by all species, with diatoms second in importance. Mineral particles, filamentous algae and animal tissue were generally present in only trace amounts.

Material consumed was dependent upon availability in the microhabitat where nymphs fed. Most ephemeropteran species, or certain size classes of a species, could be placed in one of two major food habit regimes. "Surface Feeders" consumed large amounts of diatoms, especially epilithic diatoms. The nymphs ingested high proportions of small particles, with total volume of consumed material being below average. "Interstitial Feeders" contained uniformly low proportions of

predominantly epipelic diatoms in their guts. The nymphs ingested greater quantities of large particles, and the total volume of gut material fluctuated by species.

Very small nymphs of some populations ingested higher than average quantities of detritus; this likely reflects food availability in the interstitial habitat where the nymphs hatch.

Seasonally, the detrital food base was often most important during late winter and spring. Diatom ingestion was elevated amongst surface feeders during spring and autumn, if epilithic diatom standing crops increased at that time.

Average detrital ingestion was greatest in the brown-water stream (Bigoray River), whereas diatoms were proportionally most important near the headwaters of the agricultural stream (Stauffer Creek).

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My wife Susan should receive co-authorship on this thesis for all the hours she spent calculating and typing. Thank you for putting up with a constantly distracted graduate student for four years.

Lastly, I am appreciative to the thousands of mayflies who contributed their gut contents in the name of science.

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INTRODUCTION

Impetus for this study was derived from interest in the relative importance of heterotrophic versus autotrophic production as comparable food bases for stream invertebrates. A review by Cummins (1973) of the trophic relations of aquatic insects concluded that detritus was the trophic base of most aquatic systems. Workers dealing specifically with lotic systems found that allochthonous organic material was often the most important food resource for aquatic organisms (Jones 1950, Chapman and Demory 1963, Minckley 1963, Coffman 1967, Gilpin and Brusven 1970, Shapas and Hilsenhoff 1976). Most of these studies were carried out on streams located in forested temperate watersheds. The need for a comparative study of different "kinds" of watersheds from a similar latitude seemed apparent. I chose immature ephemeropterans as the study group because they are almost entirely herbivore-detritivores, and they are abundant and diverse in most streams.

My literature review indicated a need for a detailed food habit analysis during all seasons. Muttkowski and Smith (1929), who undertook the first detailed study of food habits of aquatic insects, concluded that "local conditions begat local results"; and Cummins (1973) suggested that this is still the basic premise

of aquatic trophic relations. If so, seasonal changes in availability of food items and ingestion patterns should be important to successful completion of the life cycle as well as to the general ecology of the lotic invertebrates.

In many of the food habit studies that have been reported, sampling had been carried out on only one or a few dates during the year; this makes detection of food habit changes during nymphal development impossible. I also felt that sampling throughout the year was needed to detect differential ingestion of food items between nymphal size classes.

In previous food habit studies, gut analysis techniques were based entirely on microscopic examinations, and these analyses do not accurately quantify the size range of particles nor the total volume of material consumed. Ingestion of different size particles by zooplankton species has been found important to their trophic ecology. Similarly, I postulated that ingestion of different size particles amongst different mayfly species, different populations of the same species, or different size classes within a population may be related to the nymphs' developmental stage or habitat. It was hoped that by use of an electronic particle counter these parameters could be accurately quantified.

Four locations on three different streams were chosen as study sites (Fig. 1). Stauffer Creek is a springfed stream located in a predominantly agricultural watershed. An upstream site was chosen because of its close proximity to the headwaters, its constant thermal regime (no winter ice-cover) and its expected minimal input of allochthonous organic material. I postulated that autotrophic production could be very important to benthic populations at this site. A second site further downstream on Stauffer Creek was chosen to determine if increased organic input produced by the larger watershed area would result in a different trophic regime.

A brown-water stream, the Bigoray River, was selected because of the large quantity of allochthonous organic material the stream receives. My initial hypothesis was that ephemeropterans of this stream may be very dependent on detritus.

The third stream chosen was located in a mixed deciduous-coniferous foothills watershed. The Tay River is a fast-flowing stream, supporting relatively large epilithic algal populations and diverse benthic invertebrate populations. I postulated that a high availability of detrital and algal material might result in a wide range of food habits in this stream.

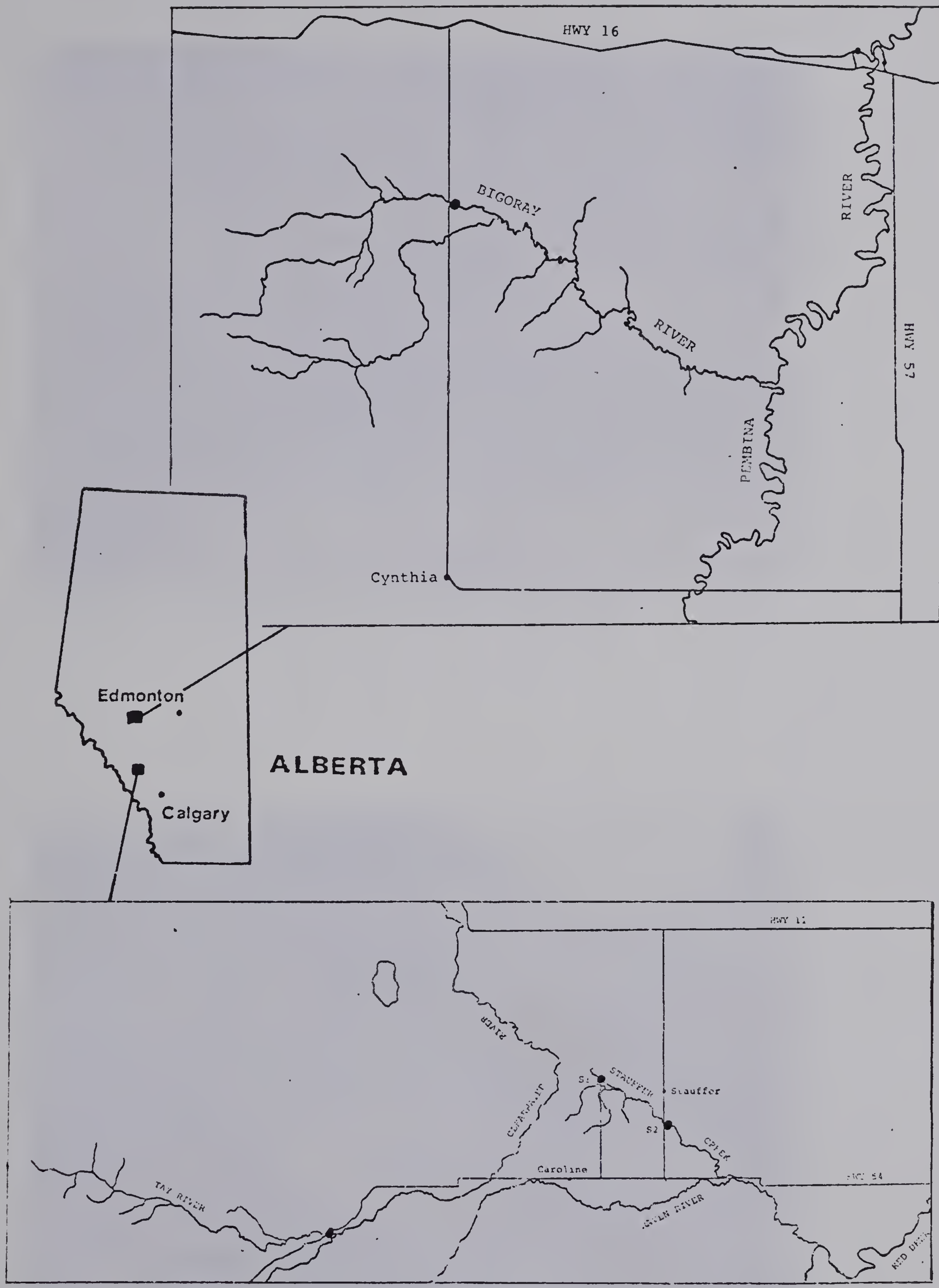

Figure 1. Streams studied with sampling sites indicated by dots.

Plate 1. Bigoray River Sampling Site.

Plate 2. Tay River Sampling Site.

Plate 3. Stauffer 1 Sampling Site.

Plate 4. Stauffer 2 Sampling Site.

SITE DESCRIPTIONS

Bigoray River

General

The Bigoray River area has been previously described in detail by Clifford (1978) and will be only briefly summarized here. It is a brown-water, muskeg stream located in west central Alberta (53°31'N, 115°26'W), approximately 145 km west of Edmonton (Fig. 1). The Bigoray River, part of the Arctic Ocean drainage, flows into the Pembina River, which in turn drains into the Athabasca River. The climate of the area is microthermal according to the Koëppen classification (Longley 1972). Average annual air temperature of the area is 4°C and the average total precipitation is 45 cm/year.

Bedrock of the Bigoray watershed consists of sandstone and soft shale. The soils of the area consist primarily of poorly drained organic soils, of which sedge peat is the most abundant followed by some *Sphagnum* and feather moss types.

Dominant trees of the watershed are black spruce (*Picea mariana*) and willows (*Salix* spp.), with some stands of tamarack (*Larix laricina*), aspen poplar (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*).

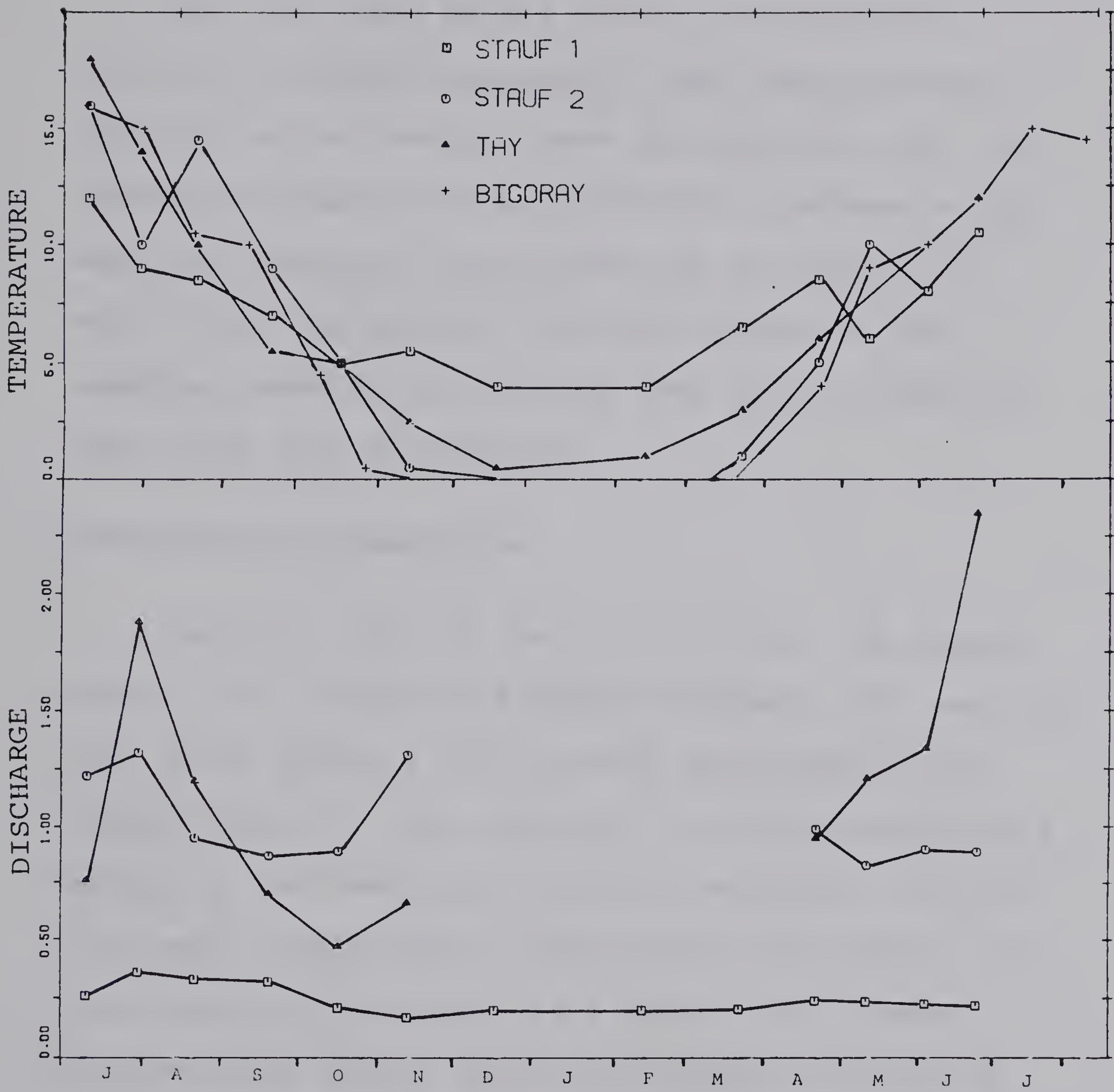

Figure 2. Temperatures (°C) and discharges (m^3/sec) recorded on each sampling date (1975/76).

Morphometric Features

The total area of the Bigoray watershed is 455 sq km (largest watershed of the three studied), with 87.3 sq km located above the sampling site. The length of stream is 76 km with 32 km upstream of the sampling location. The altitude at the source is 945.2 m and the gradient from the source to the sampling location is 3.1 m/km. The stream length to area ratio is 0.37 km/sq km.

Sampling Site Description

The north fork of the Bigoray River was sampled where it is crossed by Secondary Highway 753. Sampling took place within a 50 m stretch downstream of the bridge (Plate 1). The substrate in this area consists mainly of sand and silt, which is partially overlain with small gravel and in some areas with rubble. In cross section the stream is u-shaped with almost perpendicular banks. There are extensive growths of riparian willows; however the study site would be considered open with no canopy.

Physical Chemical Characters

The temperature regime of the stream (Fig. 2) is characterized by a summer high of 16-18°C and a winter temperature of near 0°C for about 5 months. The stream

Table 1. Water chemistry data - quarterly averages.

		Dissolved Oxygen % Saturation	Conductivity (Micromhos)	Total Residue (mg/l)	Color	Turbidity (JTU)	Total PO_4 (mg/l)	Orth PO_4 (mg/l)	Organic PO_4 (mg/l)	Organic Nitrogen (mg/l)	Nitrate Nitrogen (mg/l)	Total Hardness (mg/l)	Ca Hardness (mg/l)	pH	Total Alkalinity (mg/l)	Phenl. Alkalinity (mg/l)
BIGORAY	JFM	50	427	318	30.0	11.1	0.22	0.14	0.02	0.12	0.15	242	130	7.73	232	0
	AMJ	69	161	186	168.0	2.8	0.49	0.24	0.05	0.33	0.07	113	63	7.74	96	0
	JAS	77	187	171	208.0	31.0	0.31	0.10	0.09	0.51	0.06	145	80	7.71	110	0
	OND	53	316	239	105.0	6.7	0.31	0.15	0.07	0.15	0.05	184	109	7.71	176	0
STAUFFER 1	JFM	83	393	297	6.0	3.2	0.14	0.05	0.06	0.08	0.09	266	165	7.79	153	0
	AMJ	98	370	326	18.2	1.1	0.32	0.17	0.04	0.15	0.09	281	183	7.88	163	0
	JAS	105	420	297	2.2	7.0	0.15	0.0	0.08	0.25	0.06	247	140	7.84	136	0
	OND	85	386	284	0	16.5	0.19	0.06	0.05	0.14	0.07	231	132	7.52	133	2.0
STAUFFER 2	JFM	72.7	414	306	12.5	5.6	0.18	0.05	0.10	0.16	0.10	272	167	7.68	180	0
	AMJ	90.7	380	338	36.5	3.1	0.36	0.20	0.08	0.40	0.04	297	184	7.96	199	1.8
	JAS	102.3	393	304	5.0	7.2	0.12	0.13	0.05	0.18	0.02	231	121	7.86	138	0
	OND	73.5	378	316	2.0	15.5	0.16	0.07	0.02	0.17	0.09	226	128	7.34	141	0
TAY	JFM	90.4	362	252	3.0	5.2	0.20	0.08	0.07	0.01	0.12	235	150	7.77	184	0
	AMJ	94.0	220	223	32.8	1.9	0.39	0.16	0.09	0.16	0.05	158	102	7.90	130	1.05
	JAS	94.6	299	222	14.5	4.6	0.15	0.13	0.08	0.25	0.03	169	98	8.14	137	0.6
	OND	92.9	328	237	4.0	3.1	0.16	0.0	0.04	0.04	0.06	193	112	7.48	144	0

froze over on ca. 20 October 1975 and remained frozen until the first week in April 1976. The maximum depth of ice recorded was 50 cm and occurred during March.

Average discharge values for the Bigoray River have been reported by Clifford (1978). Winter flows are very low and the stream is usually ice-covered from mid-November to early April. Peak discharges usually occur in April and May (1.5-2.0 m^3/sec); flow remains quite high during May and June, and then declines steadily during summer and autumn. A beaver dam raised the mean water depth and decreased the flow during late summer and autumn 1975. The dam was removed in early spring 1976.

In contrast to many brown-water streams, the Bigoray River is a hardwater stream with a high bicarbonate alkalinity and pH consistently above 7.0 (Table 1). Many muskeg streams are acidic because they drain organic soils of *Sphagnum* and feather moss origin; in contrast, the Bigoray watershed consists mainly of sedge peat soils. The high color values attest to the brown nature of the water, resulting from leaching of humic substances from the watershed. Total dissolved solids and calcium hardness for the Bigoray River were generally not as high as that found in the other streams; this is possibly due to its marshy drainage area. Of the three streams investigated,

the highest nutrient levels were achieved in the Bigoray River.

Stauffer Creek

General

Stauffer Creek is a springfed stream flowing through agricultural land in west central Alberta (52°012'N, 114°42'W), approximately 260 km south and west of Edmonton (Fig. 1). The stream flows into the Red Deer River and ultimately into Hudson's Bay. It is situated in the microthermal climatic zone according to the Koëppen classification (Longley 1972). Average mean air temperature of the area is 3°C with an average total precipitation of 54.3 cm and average snowfall of 177.0 cm.

Soils of the area consist of some sedges and peat moss in the low marshy areas adjacent to the stream, while podzolic grey wooded soils predominate in the remainder of the watershed. Some areas of degrading-black earth are found near the headwaters.

Vegetation of the watershed is characterized by grasses and sedges interspersed with willows and alder spp. in the marshy areas below site 1. The headwater area is characterized by pasture and cereal crops, with some balsam poplar and aspen poplar in

the areas not under cultivation. The north side of the watershed is cultivated for pasture, hay and cereal crops, with stands of aspen and balsam poplar in the naturally vegetated areas. The south side of the watershed has little agricultural land, except for a small amount of pasture. It is characterized by black spruce (*Picea mariana*) in the lower areas and a gradual transition to white spruce, interspersed with aspen poplar at higher elevations.

There is extensive grazing in the watershed, especially in the areas adjacent to the stream. This certainly increases the nutrient input to the stream from surface runoff and also causes a siltation problem due to bank erosion.

Morphometric Features

Stauffer Creek has a total watershed area of 131 sq km with a total length of 18.8 km. It originates from two springs each having a discharge of approximately 0.17 m^3/sec; these are in turn supplemented by a number of other springs within the first few hundred meters of the source. The altitude at the source is 993.2 m. Study site 1 was located 1.5 km downstream from the source. The area of watershed above site 1 is 4.5 sq km, the gradient from the source to the site is 3.1 m/km, and the stream length to area ratio is 0.33 km/sq km.

Study site 2 was located 10.8 km downstream from the source and drains 96.8 sq km. The gradient from source to site 2 is 2.9 m/km, and the stream length to area ratio is 0.11 km/sq km.

Sampling Site Description

Site 1 was located downstream from a gravel secondary road. Immediately below the road culvert the stream forms a pool which in turn opens into a riffle. Below the riffle a shute follows the road for approximately 100 m before it turns to the south-east (Plate 3). At site 1 the stream is 7-8 m wide and is characterized by two types of substrate. The riffle and pool area immediately below the culvert, where the samples were collected, has a substrate of medium sized pebbles and small gravel. The other substrate type consists of silt deposits formed both upstream of the site (before it crosses the road) and in the shute area below the riffle. During summer, dense beds of Hippurus vulgaris develop in these silt deposits. These silt beds interspersed with riffle areas are characteristic of Stauffer Creek's upper 4 km. The canopy in the vicinity of site 1 and upstream to the headwaters is completely open.

Stauffer site 2 was located where the stream flows through a pasture approximately 300 m downstream

from a bridge (Plate 4). The samples were collected within a 50 m section between two bends. The stream is 6-7 m wide at this location and varies from 25 to 30 cm in depth, except for a deeper pool at the site's downstream end. The stream bottom at site 2 is composed of medium sized pebbles and small gravel. In contrast to site 1, travertine deposits developed on the rocks, and silt and sand deposition occurred in the riffles; and there were no silt beds or extensive growths of Hippurus. The site 2 area supported extensive growths of riparian willow and alders; however, they do not form a complete canopy over the stream.

Physical Chemical Characters

Stauffer Creek's springfed origin results in physical and chemical attributes not present in the other streams investigated. The most unique feature is the temperature regime (Fig. 2). Water at the springs' sources has a temperature of about 6°C, and this has a stabilizing effect on water temperatures at site 1. At site 1, summer temperatures are lower than at site 2 (and also lower than the water temperature of the other two streams), while winter water temperatures are considerably higher than at site 2. Furthermore, as a result of the warmer water in winter, the upper reaches

of Stauffer Creek do not freeze over. Site 2 has a more typical temperature regime for this latitude, exhibiting higher summer temperatures than at site 1; winter temperatures are near 0°C. Site 2 is ice-covered from approximately the end of November to the first week of April, with maximum ice thickness of about 80 cm.

Stream discharge (Fig. 2) for Stauffer is quite stable because of its springfed origin. Flow at site 1 was consistent at approximately 0.2 m^3/sec, except for a slight increase during the summer months. Discharge at site 2 is more variable and generally higher than site 1, fluctuating between 0.85 and 1.3 m^3/sec. This is probably due to the greater influence of surface runoff at site 2.

Stauffer Creek is a hardwater stream with a high bicarbonate alkalinity, which in turn results in a fairly uniform pH of about 7.8 (Table 1). Total dissolved solids and calcium hardness are generally higher than for the Tay and the Bigoray Rivers, again possibly due to Stauffer's spring origin. There are some marl deposits at site 2.

Tay River

General

The Tay River is a foothills stream on the east slopes of the Rocky Mountains of west central Alberta (52°03'N, 115°06"W). It is located approximately 280 km southwest of Edmonton (Fig. 1). The stream drains into Hudson's Bay via the Clearwater and North Saskatchewan Rivers. Climate of the area is classified as micro-thermal according to the Koëppen classification. Average mean air temperature of the area is 2°C with average total precipitation of 64.1 cm; average total snowfall of the area is 229.1 cm. The sampling site was located near the stream's confluence with the Clearwater River.

No soil survey has been carried out in the Tay River area; however the region appears to be characterized by sedge and peat moss in the lowlands. Vegetation of the upper two-thirds of the drainage basin consists mainly of white spruce, with some lodgepole pine (*Pinus contorta* var. *latifolia*). The lower third of the watershed is dominated by a mixed forest of white spruce and aspen poplar. Low marshy areas adjacent to the stream, dominated by sedges and grasses interspersed with willow, alder, and some dwarf birch, make up about 4% of the watershed.

There is no evidence of logging or farming in

the watershed; however, there are a few summer cottages immediately upstream of the sampling site.

Morphometric Features

Total watershed area is 239 sq km, with 237 sq km being upstream of the sampling site. Altitude at the source is 1676.4 m and the gradient from source to the sampling site is 13.2 m/km. Total length of the stream is 37 km with 36.5 km of the stream being upstream of the sampling location. The ratio of stream length to watershed area is 0.15 km/sq km.

Sampling Site Description

The sampling site was located at a provincial campsite, where Highway 54 crosses the Tay River. Samples were collected in a riffle approximately 25 m downstream of the highway bridge (Plate 2). The river at this point was about 6 m wide and from about 15 to 30 cm in depth. There was little vegetation on the banks in the immediate sampling area because of clearing for the campsite and bridge. Immediately upstream and downstream of the sampling site, the river flows through a thick mixed white spruce and aspen poplar forest, which creates a substantial canopy over the stream and in many locations almost completely closes it over. The stream bottom consisted of medium sized cobbles, pebbles, and gravel lying on top of sand. This type

of substratum was general throughout the stream, even in the deeper reaches, and is due to the fast flow and high gradient of the stream.

Physical Chemical Characters

Winter water temperatures of the Tay River are not as low as for the Bigoray and Stauffer site 2 (Fig. 2). The winter of 1975-76 was particularly mild and the Tay River was ice-covered from approximately December first until mid-March; however the riffle from which the samples were taken never completely froze over.

Discharge varied from 0.5 m^3/sec to 2.0 m^3/sec, with peak flow, due to mountain snow melt and heavy June rains, in late June and early July 1976. Flow fluctuated more than in Stauffer Creek.

The Tay River is also a hard water, high bicarbonate-alkalinity stream (Table 1). Its total dissolved solids and calcium hardness were intermediate between those of Stauffer Creek and Bigoray River. The Tay River consistently had the highest percent oxygen saturation of the three streams, due to its shallow depth and fast flow.

MATERIALS AND METHODS

Regular sampling of the four sites, from early July 1975 until early August 1976, was undertaken at approximately 3-week intervals. During winter, the sampling interval was lengthened to about 6 weeks.

Flora

Changes in epilithic diatom standing crop were determined on each sampling date by collecting and preserving in 10% formalin between 5 and 10 rocks exposed at the substrate's surface. In the laboratory, diatoms were removed by scraping the entire surface of each rock with a stiff brush. The scrapings, along with the formalin in which the samples were stored, were deposited in a beaker and allowed to stand for 24 hours. During this period the diatoms settled to the bottom and the formalin could then be siphoned off. Each sample was then treated with a mixture of concentrated sulphuric acid and potassium dichromate to clear the frustules. The digestion agent was removed by a series of seven distilled water rinses using the same routine as for removal of the formalin preservative. Two subsamples from each cleared sample were placed uniformly on 22 mm diameter cover slips, dried at a low temperature on a hot plate, inverted,

and mounted on a slide in a drop of Permount. The diatoms in a known area of each slide were then identified and counted.

Surface area of the rocks scraped was determined by covering each rock with aluminum foil. I was careful to cut off foil that was not in direct contact with the rock surface. The foil was then removed, flattened and traced onto paper, and the surface area determined with a planimeter. Total surface area of the rocks scraped for each sample was arbitrarily reduced by 25% to compensate for the area not exposed to light and therefore not populated with diatoms.

Standing crop of diatoms was calculated by multiplying the diatom count of each subsample by a conversion factor and then taking the average value of two replicates. The conversion factor was:

$$CF = \frac{Sc \times Vs}{ASs \times VSs \times Sr}$$

Sc = surface area of cover slip

Vs = volume of diatom sample

ASs = area of cover slip scanned

VSs = volume of subsample

Sr = surface area of rocks minus 25%.

Dominant macrophytes from each site were identified and an estimate of percent coverage by each

species determined. Significant growths of filamentous algae were also noted.

Sampling of Ephemeropterans

Qualitative samples of mayfly nymphs were taken at each site on each sampling date. The samples were collected with a compound dip net consisting of a coarse 1 mm mesh inside a fine 210 um mesh. Samples were collected by disturbing the substrate to dislodge the mayflies, which were then collected in the net held immediately downstream. This operation was performed at many locations throughout the sampling site. Specimens were also collected by sweeping the net through any submerged macrophytes present in the study area.

The compound net partitioned the sample into two fractions (Fig. 3). Material collected in the coarse mesh consisted primarily of large nymphs (larger than 2 mm) and organic debris. The fine mesh retained the smaller specimens, mineral material, and some fine organic debris. Both fractions were fixed in 70% ethanol to prevent regurgitation of stomach contents (Coffman 1967). The ethanol was then filtered off immediately and the samples preserved in 15% formalin. Formalin was used instead of ethanol because formalin

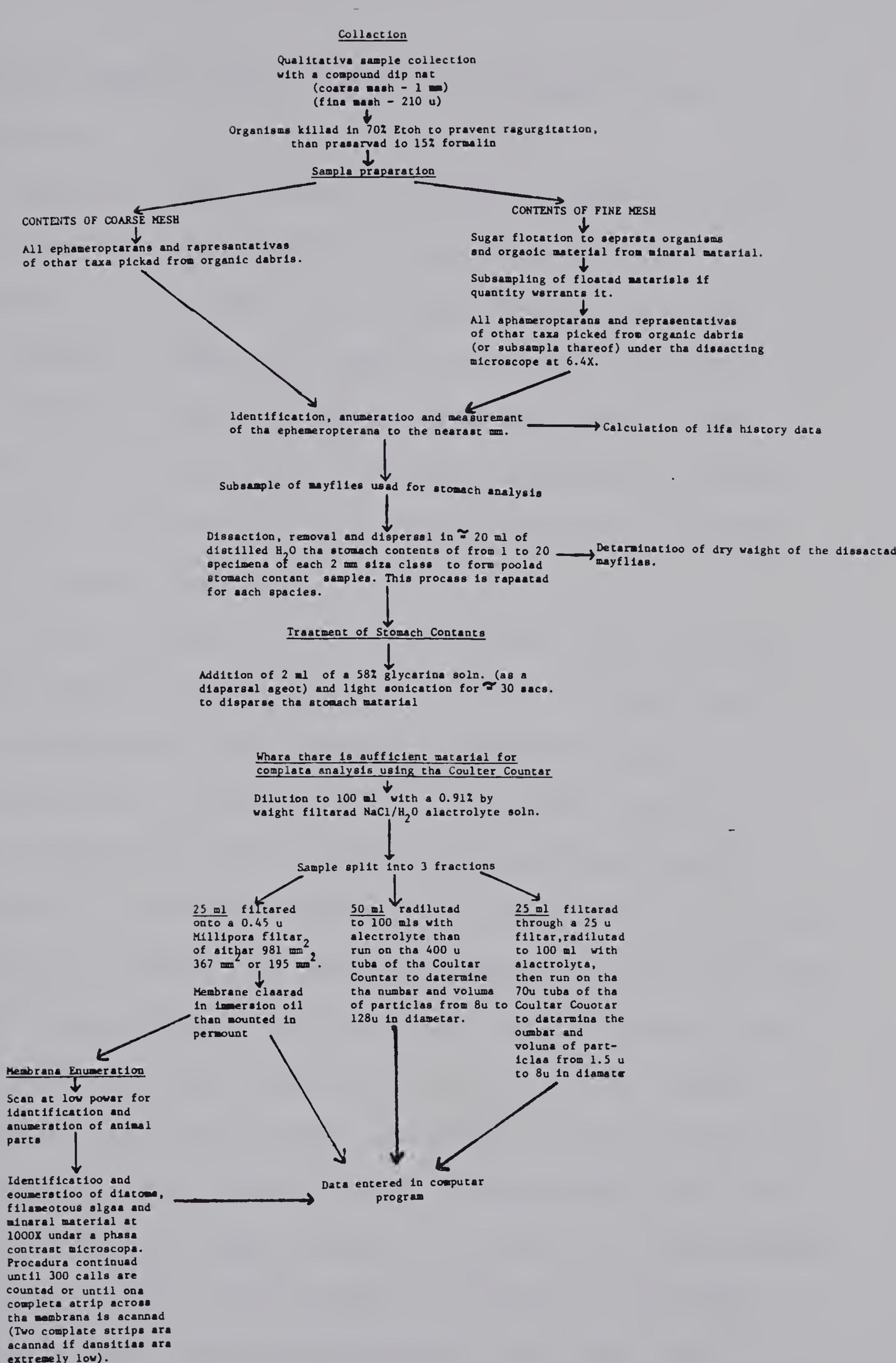

Figure 3. Summary of stomach analysis methods.

reduced leaching of pigments from ingested plant materials.

Mayflies were removed from the coarse fraction of the sample by suspending small amounts of the material in an enamel pan. Sugar flotation, using the method of Anderson (1959), was used to extract the ephemeropterans from the fine fraction of the sample. This flotation technique worked well because the major portion of the organic debris was removed by the coarse mesh.

If the number of mayflies in the fine fraction of the sample was greater than 2,000, the specimens were subsampled after flotation. The subsampler consisted of a gallon glass jar with the bottom partitioned into eight equal pie-shaped quadrants. Specimens in the subsampler were suspended in a dilute solution of ethanol to prevent flotation. Once settled, nymphs were removed from the quadrants by aspiration.

Mayflies from both the coarse and fine sample fractions were identified, counted, and separated into millimeter size classes based on measurement of total length (front of head to base of cerci). All specimens from the coarse fraction were counted and measured. Quadrants from the subsampled fine fraction were successively analyzed under a dissecting microscope at 6.4X until at least 300 specimens were counted.

To associate the mayfly nymph with the adult stages (adults are needed for species identification), nymphs were reared in the laboratory. The 4-litre containers were aerated with the opening sealed with cheese cloth, and a twig, projecting out of the water, was placed in each container. The nymphs crawled onto the twig when emerging. The containers were kept at 15°C in a circulating water bath, and subimagoes were removed as they emerged. Subimagoes were allowed to transform into imagoes and then preserved in 70% ethanol.

Stomach Analysis

A stomach analysis sample consisted of stomach contents of a pooled sample for each 2 mm size class. Number of individuals used in a stomach analysis depended on total length of nymphs (from about 20 specimens for the 2 mm or less size class to 3 or 4 specimens for an 8-10 mm size class).

Stomach contents were removed from the specimens by microscopic dissection in a watch glass containing distilled water. Contents were removed either by splitting the specimen in the thoracic region and teasing the contents out of the digestive tract or by removing the gut intact before breaking the digestive tract and removing the material. Contents were removed

from the watch glass with a micro-pipette and deposited in a clean vial containing approximately 20 ml of distilled water. Care was taken to suck up only material present from the stomach and not pieces of body tissue.

Analysis of the pooled gut content samples was carried out using a combination of Coffman's (1967) membrane filter technique and an electronic particle counter (Fig. 3). The problem with previous invertebrate stomach analysis techniques has been the inability to quantify accurately the volume of detrital material. All techniques relied upon a two-dimensional estimate of food components under a microscope. These techniques are adequate for materials such as diatoms and filamentous algae, which have rigid and uniform shapes. However, for the detrital component, which is amorphous and greatly variable in its dimensions, I felt a more accurate method was required.

An electronic particle counter, namely a Coulter Model TA II, was used to measure the total number and volume of ingested particles from each stomach contents sample. Theory of electronic particle sensing is based on breaking of an electronic field as the particle passes through an aperture. A subsample of particles from the mayfly stomach contents was dispersed in a beaker of electrolyte (0.9% by weight NaCl in distilled

H_2O). A glass tube having a small aperture was also suspended in the beaker along with an electrode. A second electrode, at ground potential, was located on the inside of the tube. A constant current was supplied to the external electrode (in the sample beaker), and this results in a current flow from the external electrode through the aperture to the ground electrode inside the tube. The electrolyte, with particles suspended in it, is drawn through the aperture by a vacuum established inside the tube. As a particle passes through the aperture, it momentarily increases the resistance and reduces the current, the amount of current change being proportional to the size of the particle. The machine records each change in current as a particle count and interprets the particle volume from the magnitude of the current change.

The counter provides a proportional breakdown of the total volume of material measured into size class channels. The mean volume of the particles recorded in each channel is exactly twice that of the preceding channel. It is possible to calculate the number of particles measured in each size class channel.

A particular counting tube will accurately measure particles having diameters between 2 and 40% of the diameter of the aperture. For example, a tube with a

70 um aperture will accurately measure particles having diameters from 1.4 um to 28 um. I found that a range of measurement from 1.59 um to 160 um in diameter (2.09 to 2,196,000 um^3) was adequate for mayfly stomach analysis. The amount of material with a diameter below 1.59 um was extrapolated to be less than 1 or 2% of the total, and particles larger than 160 um were seldom encountered. For analysis in this range, I used two aperture tubes: a 70 um aperture tube measured particles having diameters from 1.59 um to 8.0 um, and a 400 um tube measured particles from 8.0 um to 160 um.

Once stomachs were dissected and placed in the vial of distilled water, 2 ml of a 50% glycerine solution (filtered through a 0.45 um membrane filter to remove all particles) was added and shaken vigorously to dissociate the stomach particles. This process was aided by sonication with an immersion type sonicator for approximately 30 seconds. I found this to be the proper interval to break down most large aggregates of particles without breaking the particles themselves. The sample was then placed in a volumetric flask and diluted to 100 ml with 0.9% NaCl electrolyte. All glassware was carefully washed and rinsed with distilled water, and the electrolyte was filtered through a 0.45 um membrane filter immediately before use to remove possible particle contamination. The sample was then

randomly separated into three fractions, one to be filtered onto a membrane filter and the other two to be used for electronic particle analysis. The amount of the sample going into each fraction was carefully noted; hence I could back calculate to a per sample and per stomach basis.

The same mounting technique that Coffman (1967) used for gut analysis was used for the fraction filtered onto the 0.45 um membrane filter. The filter was cleared in immersion oil in an oven at 35°C and then mounted in Permount on a glass slide. This portion of the sample was used for determining the number and kinds of diatoms contained in the stomachs, the volume of filamentous algae and sand grains present, and the presence or absence of animal material. Filter analysis consisted of an initial random scan at 100X for the presence of animal material; this was followed by scanning a strip across the middle of the membrane at 1000X. All diatoms encountered during the high power scan were identified and counted. The volume of any filamentous algae was also determined during the high power scan. The mean diameter of all sand grains encountered was recorded and their volumes calculated. I assumed their shape was approximately a sphere. If the number of diatoms encountered in the 1000X scan was high ($\geq$ 300), the scan was stopped before the

complete diameter of the membrane was crossed. The number and taxa of diatoms, volume of filamentous algae, and volume of mineral material present in the initial stomach sample could then be calculated by knowing the area of membrane filter scanned, the total membrane area, and the portion of the sample filtered onto the membrane.

Efficiency of the membrane filter technique has been tested by Gray and Ward (in press). They statistically determined that gut material was randomly dispersed on the membrane and that confidence limits of 15% could be achieved on diatom counts from cleared filters.

One sample fraction used for the particle counter analysis was run through the 400 um aperture tube and the other through the 70 um aperture tube. A record of what proportion of the initial stomach sample was allocated to each fraction was again kept so that back calculations could be made. Prior to analysis on the Coulter Counter, both fractions were again diluted to 100 ml with filtered electrolyte, and the 70 um fraction was filtered through a 25 um filter to prevent aperture clogging.

Data derived from the three fractions of each stomach analysis sample were punched on computer cards and run through a Watfiv program, which I developed.

The program combined data from the 70 um and 400 um aperture tubes of the Coulter Counter to calculate the number and volume of particles in each size channel, along with the number of particles and total volume of material (expressed on a per stomach basis) for each gut sample. Due to the relatively constant size of diatoms, volume of each diatom species was calculated by taking the measurement (length, width and girdle width) of a number of individuals. Volume was determined by tracing to scale the frustule on graph paper, determining the surface area from the outline, and multiplying by the girdle width. The total consumed volume of each diatom taxon was calculated by multiplying the number per stomach (calculated from the membrane filter fraction) by the estimated volume. The program also derived the total number and volume of diatoms per stomach along with the proportion of the total volume attributed to each diatom species. Volume per stomach of filamentous algae and sand grains was similarly calculated.

Volume of detritus per stomach was derived by subtracting the volumes of filamentous algae, sand grains, and diatoms from the total volume of material determined by the Coulter Counter. Detritus was therefore defined as all remaining material present in a stomach other than diatoms, filamentous algae

and sand grains. This would include unrecognizable autochthonous and allochthonous organic material and recognizable animal tissue. The animal fraction can usually be ignored because it rarely occurred in mayflies of my study. Lastly, the program determined the proportion of each food component relative to the total. A flow chart of the entire technique is contained in Fig. 3.

The above technique could not be used for nymphs smaller than 2 mm because of insufficient gut material. An attempt to use Coffman's (1967) technique in its entirety for these very small specimens proved unreliable. I found it difficult to compare material consumed by these small nymphs with larger ones because I could not directly measure particle size or total consumed volume of food material. Analysis of material consumed by specimens less than 2 mm in length was therefore not included in my study.

Accuracy of the stomach analysis technique was tested by analyzing five replicate stomach analysis samples of 10-12 mm Siphlonurus alternatus nymphs collected on 25 June 1976. The reproducibility of the technique is good (Table 2).

Table 2. Replicate stomach analyses of 10-12 mm *Siphlonurus alternatus* nymphs collected on 25 June 1976 from the Bigoray River.

	Volume of Material Expressed in $um^3 \times 10^6$					
	Replicate					Coefficient of Variation
	1	2	3	4	5	
Diatoms	16.40	9.46	15.44	12.41	13.12	20.4%
Detritus	992.60	709.20	829.80	660.00	606.70	20.3
Mineral Particles	4.49	5.11	3.03	1.12	2.42	49.6
Filamentous Algae	0.002	0.00	0.00	0.002	0.00	-

RESULTS

Epilithic Diatom Populations

Standing Crops

Average yearly epilithic diatom standing crops varied from a low of 55,508/cm^2 at Stauffer 1 to a high of 1,514,294/cm^2 at Tay River. Bigoray and Stauffer 2 populations were intermediate at 220,317 and 529,916/cm^2 respectively. When relating diatom populations to food habit patterns, however, seasonal trends in diatom standing crop must be analyzed (Fig. 4, 5).

The "typical" pattern of epilithic diatom standing crop for temperate streams of North America and Europe is a spring maximum followed by a summer decline and a smaller autumn peak (Douglas 1958, Blum 1960, Hynes 1972, Moore 1976, Tsui 1977). The general pattern for my streams usually included a major summer or autumn maximum, with very small spring peaks. Epilithic diatoms at Stauffer 1 and Tay River sites had very low population levels in July and August, with peaks in September and October. Reduced and relatively stable late autumn and early winter populations were then established, and they remained stable through late February 1976. During March and

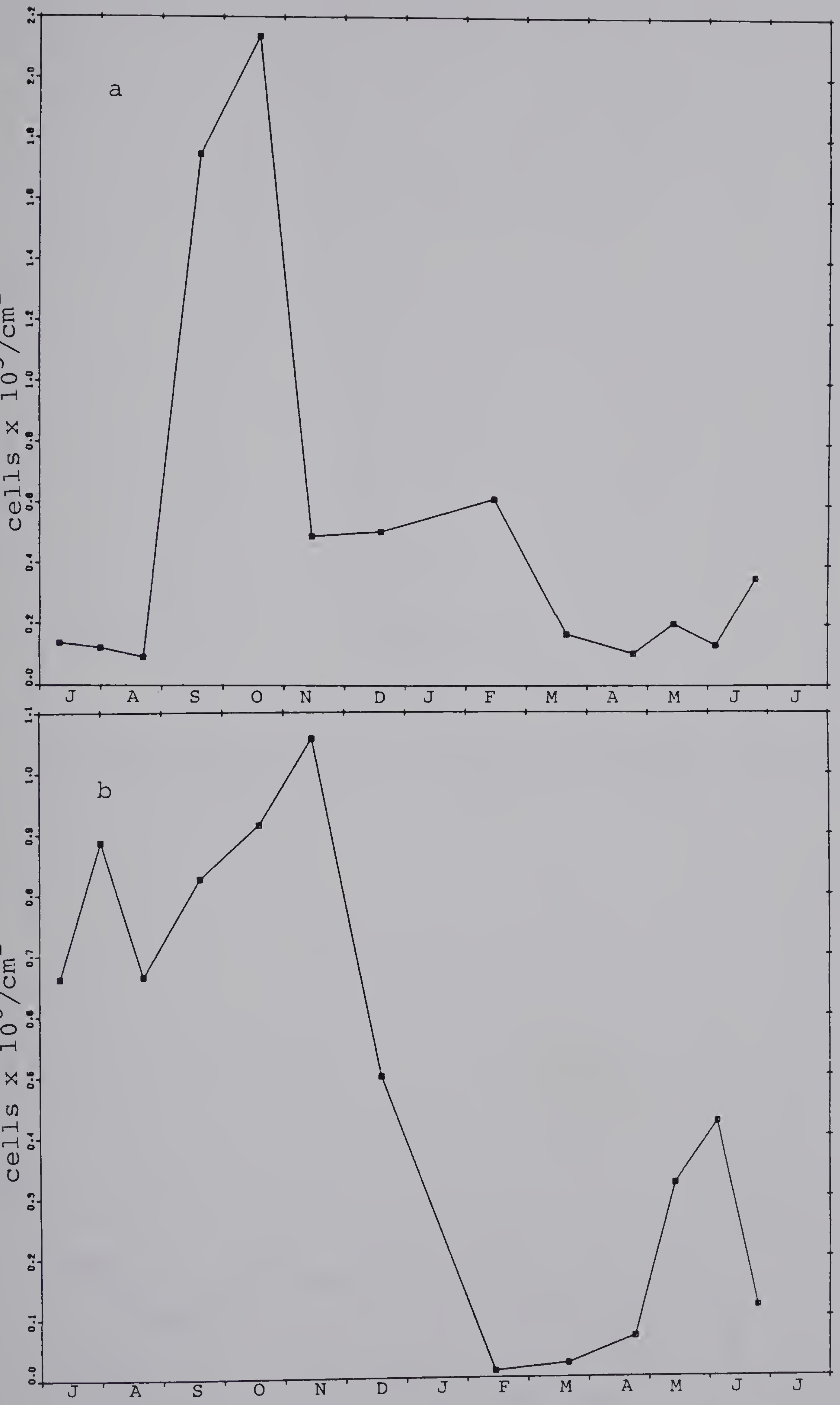

Figure 4. Epilithic diatom standing crops (1975 and 1976) - Stauffer 1 (a); Stauffer 2 (b).

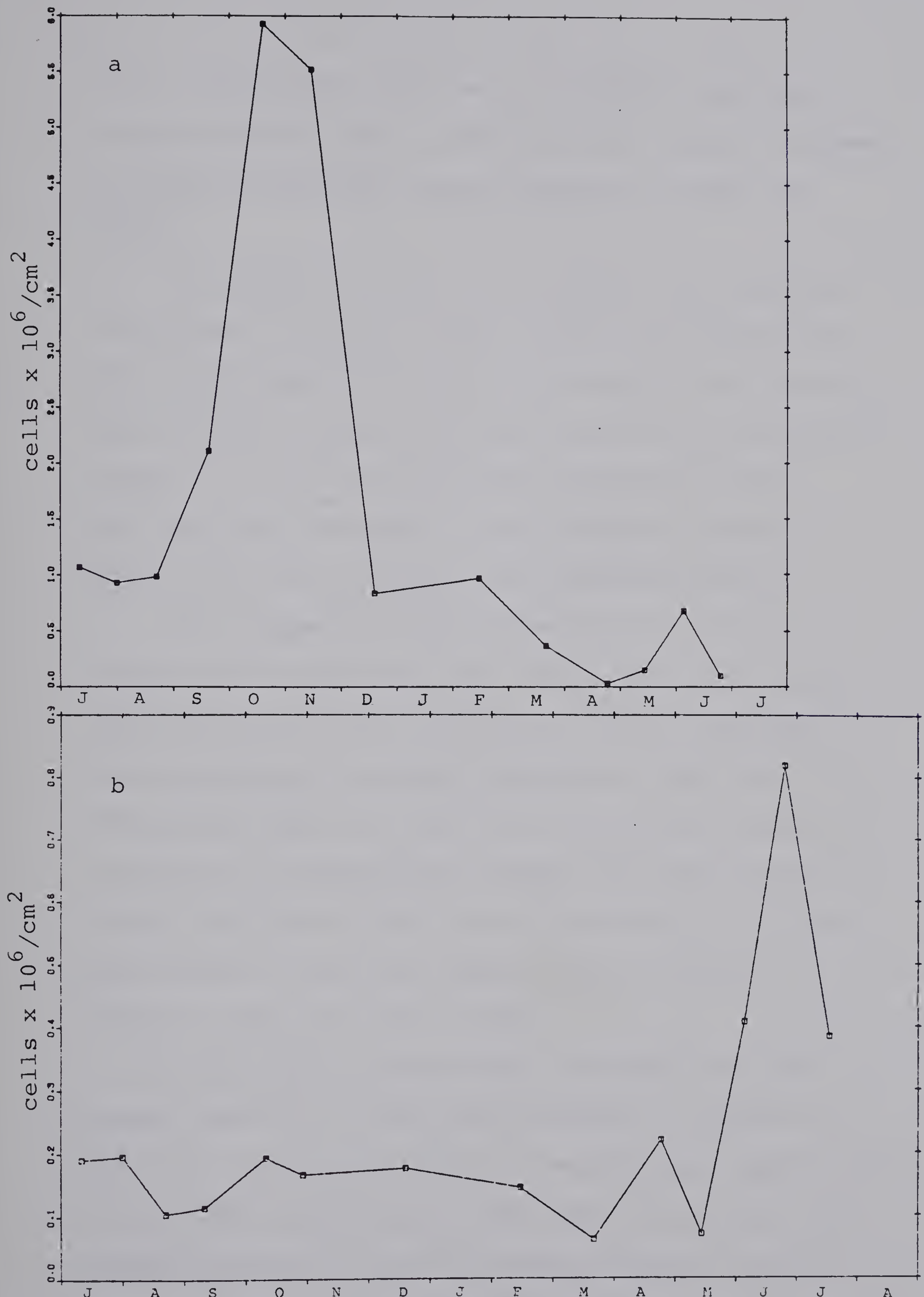

Figure 5. Epilithic diatom standing crops (1975 and 1976) - Tay (a); Bigoray (b).

April, populations declined at Stauffer 1 and Tay River to yearly lows. In May and June a small increase in diatom population levels occurred at these two sites.

The seasonal pattern of Stauffer 2 was similar to Stauffer 1 and Tay River, except for higher July and August populations and a relatively larger spring peak. Maximum population levels still occurred during autumn. A large autumn epilithic diatom peak was not detected for Bigoray River diatoms; instead a single late June and early July maximum occurred.

Three important factors controlling epilithic diatom populations are light, temperature and stream flow. Stream dwelling diatoms are often considered to have relatively low light requirements (Whitford 1960, Blum 1960, Moore 1974) and tend to optimize growth at temperatures intermediate between the summer high and winter low (Hynes 1972). High flow rates can also be detrimental to epilithic populations as shown by Douglas (1958) and Moore (1976).

At all sites investigated, extremely low late winter population levels were probably a function of low light intensities and low temperatures, particularly at Stauffer 2 and Bigoray River where extensive ice buildup occurred. Populations were probably further decimated by ice scouring and high flows during local

Table 3. Epilithic diatom species list. + indicates presence

	Bigoray	Stauffer 1	Stauffer 2	Tay
Achnanthes spp.	+	+	+	+
Amphipleura pelucida Kütz	+		+	+
Amphora sp.	+		+	
Cocconeis placentula Ehr.	+	+	+	+
Cyclotella meneghiniana Kütz.	+	+	+	+
Cyclotella spp.	+			+
Cymbella cymbiformis (Kütz.) Bréb.	+	+	+	
Cymbella sinuata Greg.	+	+	+	+
Cymbella sp.	+			
Cymbella spp.		+	+	+
Diatoma elongatum Agardh.	+	+		+
Diatoma vulgare Borg		+		+
Diatoma sp.	+			+
Didymosphenia geminata (Lyngb.)M. Schmidt				+
Diploneis sp.	+			+
Epithemia sp.				+
Epithemia spp.	+			
Fragilaria construens (Ehr.) Grun.	+	+	+	+
Fragilaria construens var. binodis (Ehr.) Grun.	+			
Fragilaria leptostauron (Ehr.) Hust.	+	+	+	+
Fragilaria leptostauron var. dubia (Ehr.) Hust.	+	+	+	+
Fragilaria pinnata Ehr.		+	+	+
Fragilaria sp.	+			
Gomphonema acuminatum Ehr.	+		+	
Gomphonema constrictum Ehr.	+	+	+	+
Gomphonema sp.	+	+	+	+
Gyrosigma sp.	+			+
Meridion circulare Agardh.	+	+		+
Navicula capitata Ehr.	+		+	
Navicula cryptocephala Kütz	+	+	+	+

Table 3. (continued).

	Bigoray	Stauffer 1	Stauffer 2	Tay
Navicula pupula Kütz	+		+	
Navicula tripunctata O.F.Müll	+	+	+	+
Navicula viridula Kütz	+		+	+
Navicula sp.	+			+
Navicula spp.		+	+	
Nitzchia spp.	+	+	+	+
Pinnularia sp.	+		+	
Rhoicosphenia curvata Kütz	+			
Rhoicosphenia sp.	+			+
Rhopalodia gibba Kütz	+			
Rhopalodia gibberula Ehr.	+			+
Stauroneis sp.	+	+	+	
Surirella sp.	+	+	+	+
Synedra amphicephala Kütz	+			+
Synedra spp.	+	+	+	+

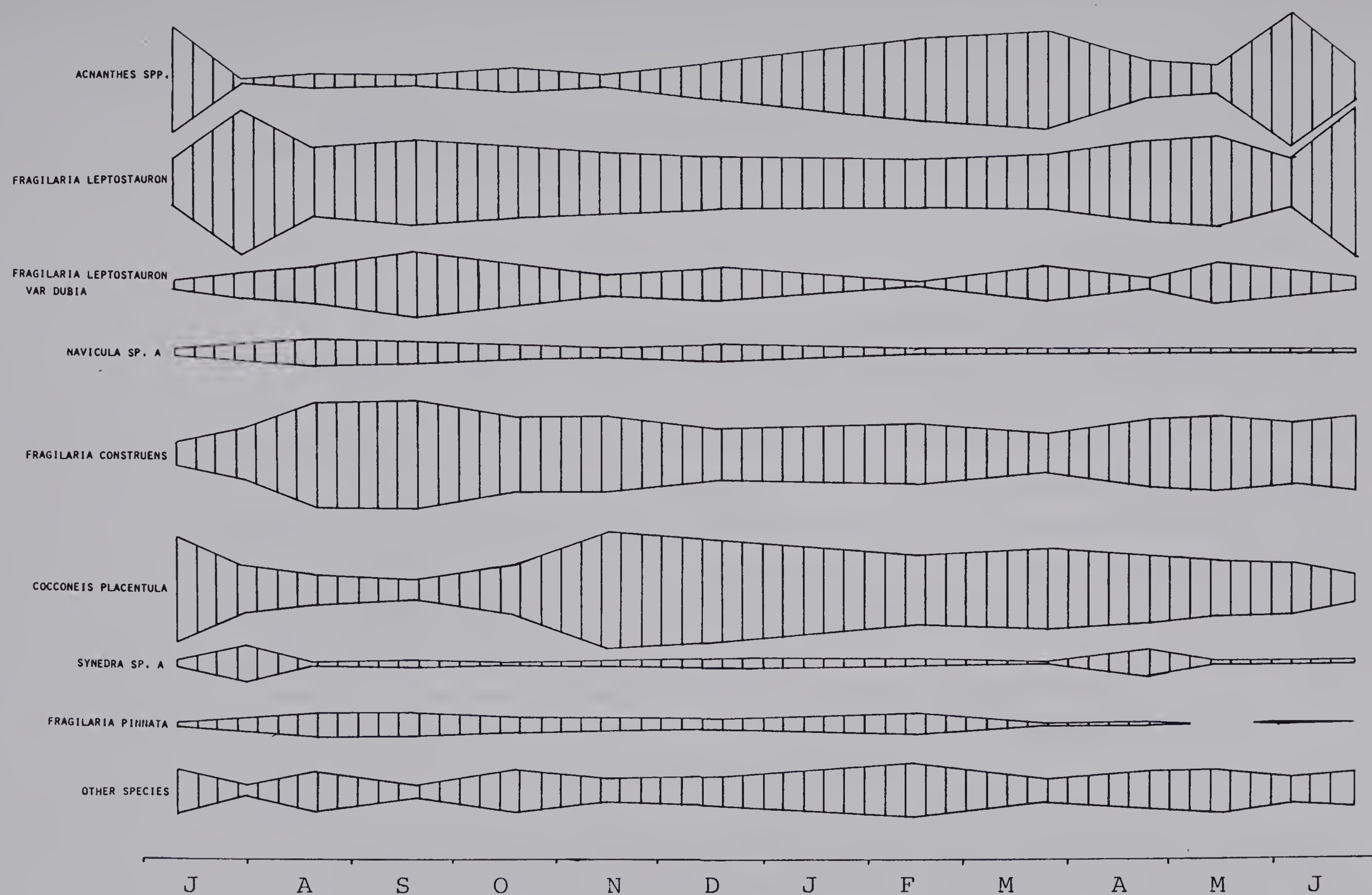

Figure 6. Proportionate abundance of epilithic diatoms - Stauffer 1. (1975 and 1976). The width of the spindle is proportional to the number of diatoms on the sampling date.

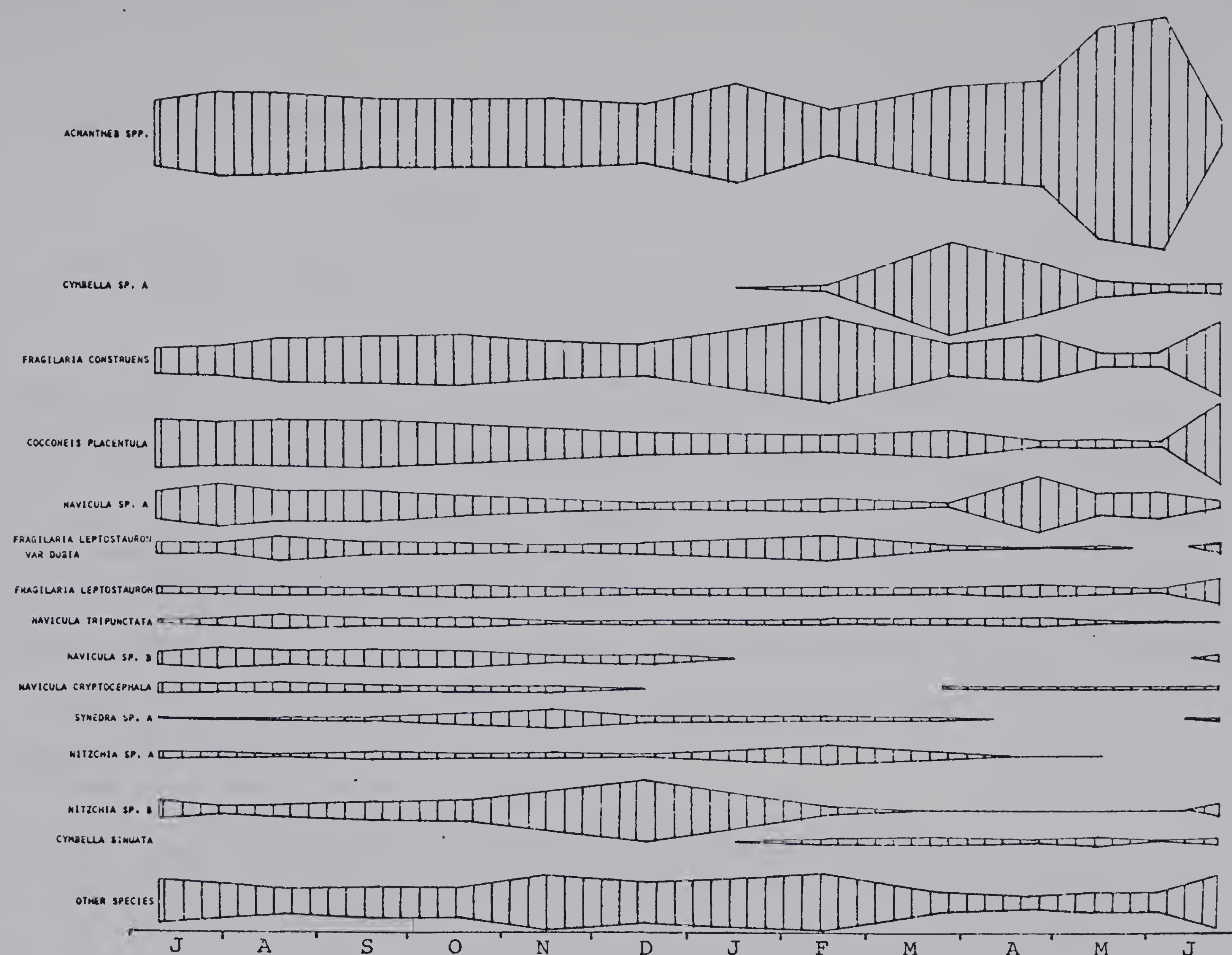

Figure 7. Proportionate abundance of epilithic diatoms - Stauffer 2. (1975 and 1976). The width of the spindle is proportional to the number of diatoms on the sampling date.

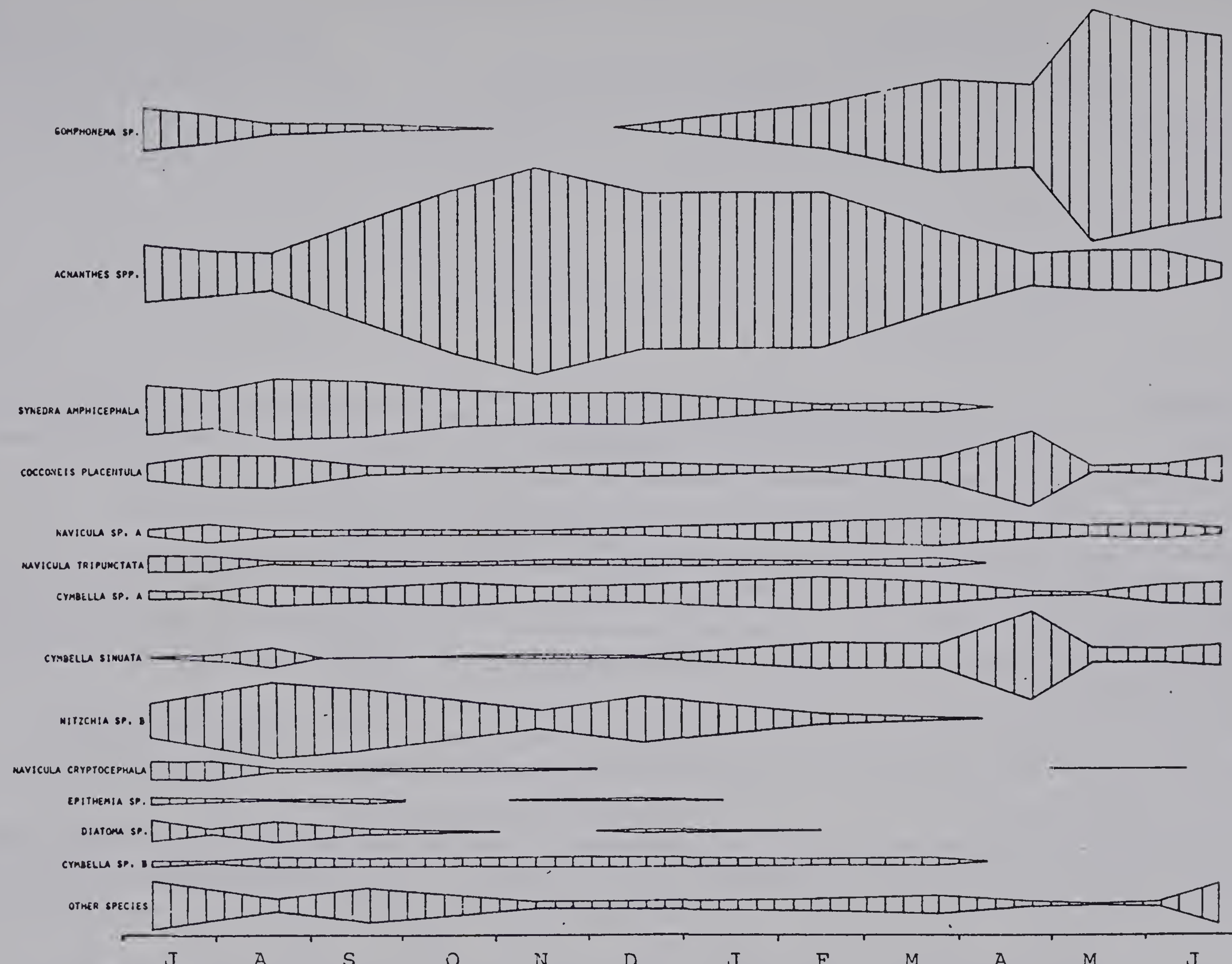

Figure 8. Proportionate abundance of epilithic diatoms - Tay River. (1975 and 1976. The width of the spindle is proportional to the number of diatoms on the sampling date.

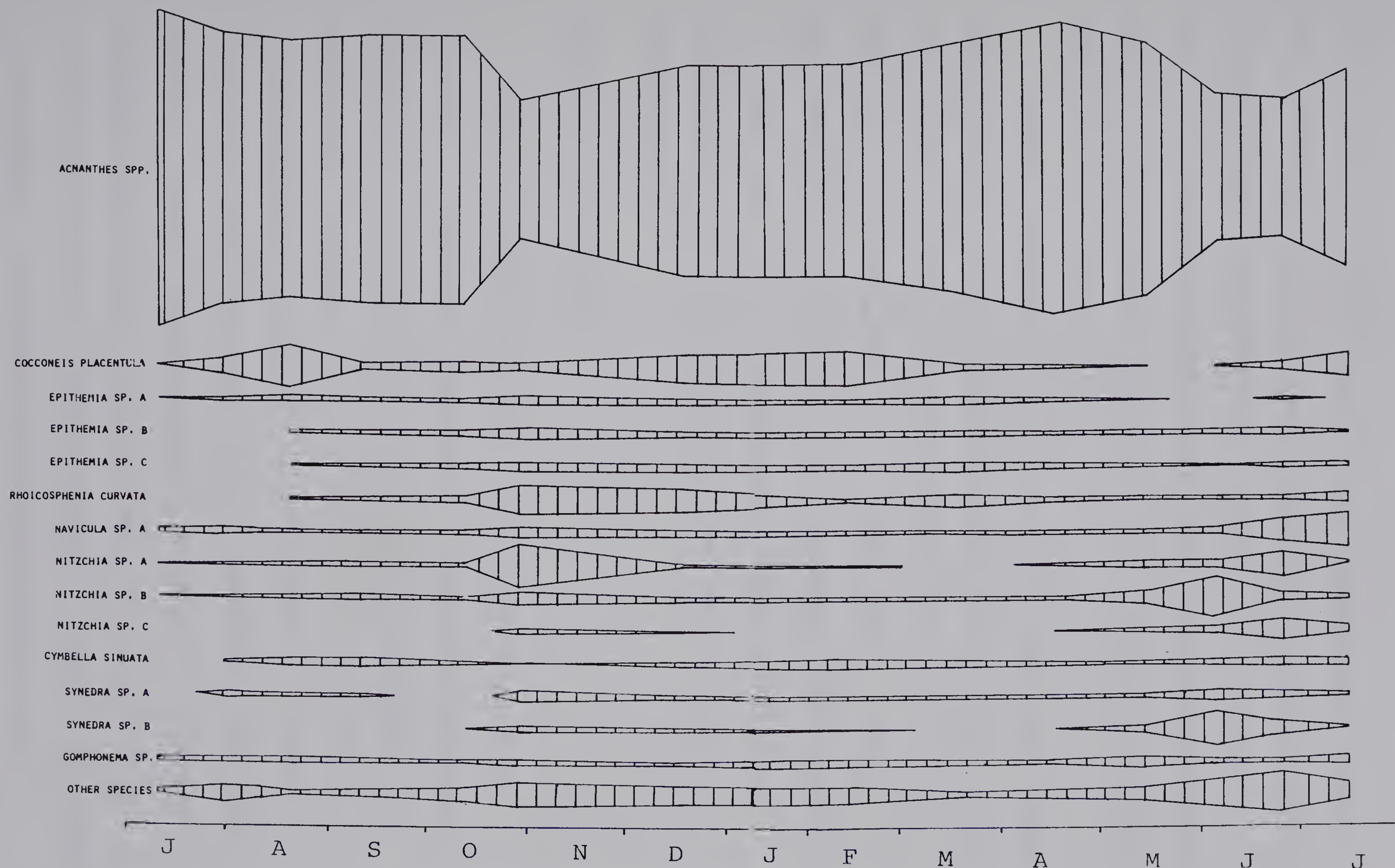

Figure 9. Proportionate abundance of epilithic diatoms - Bigoray River. (1975 and 1976). The width of the spindle is proportional to the number of diatoms on the sampling date.

spring melt. Mountain runoff and heavy rains during May and June can also result in high discharges, which Gumtow (1955) concluded can significantly depress epilithic diatom populations. High spring discharges at all sites except Stauffer 1 may explain the reduced spring diatom peak.

Autumn appears to be the optimal time for epilithic diatom growth at all sites except Bigoray River. Lack of a 1975 autumn peak in the Bigoray River may have been due to exceptionally low light levels. Beaver dam construction at that time increased water depths (80-100 cm); this in combination with high organic staining of the water may have decreased light penetration.

Species Composition

The dominant epilithic taxa enumerated from Stauffer 1 included Achnanthes, Cocconeis placentula, Fragilaria leptostauron, Fragilaria construens and Fragilaria pinnata (Fig. 6, Table 3). All except C. placentula are species associated with alkaline cold water springs (Round 1956). Compared with other sites, relative abundances were stable at Stauffer 1, perhaps reflecting a uniform temperature and flow regime at Stauffer 1. Major seasonal changes occurring at Stauffer 1 include the decreased importance of

Achnanthes sp. and C. placentula during the autumn, at which time F. leptostauron var. dubia, F. construens, F. pinnata and Navicula sp. became proportionally more abundant. The diversity of epilithic diatoms was lower at Stauffer 1 compared to other sampling sites.

There was a greater diversity of epilithic diatom species at Stauffer 2 than at Stauffer 1, and the populations exhibited more obvious seasonal abundance trends (Fig. 7). Achnanthes spp., C. placentula and F. construens were the dominant diatoms at this site. Achnanthes accounted for almost the entire epilithic population during May and early June. Other taxa showed seasonal periods of abundance; for example, Cymbella A and Navicula A had a spring growth pulse. The latter also increased in relative abundance during early autumn. Nitzchia B was a major species during winter.

The epilithic diatom species of Tay River were similar to those of Stauffer Creek except for large populations of Gomphonema sp. and Synedra amphicephala (Fig. 8). Achnanthes spp. was the dominant epilithic taxon in the Tay River throughout autumn and winter, being replaced by Gomphonema sp. during spring months. Synedra amphicephala, Nitzchia B and C. placentula were important summer species. Cymbella sinuata and C. placentula formed significant porportions of the

epilithic community during early spring.

Epilithic diatoms sampled from the Bigoray River were dominated throughout the year by *Achnanthes* spp. (Fig. 9). This species complex had a uniform relative abundance throughout the study with slight reductions during autumn and late spring. Compared to Stauffer Creek and Tay River communities, *Nitzchia* spp. and *Epithemia* spp. were relatively more important and *Fragilaria* species less important. The only taxa other than *Achnanthes* spp. to establish significant populations in the Bigoray River were *C. placentula*, *Rhoicosphenia* sp. and *Nitzchia* A during winter; and *Navicula* A, *Nitzchia* A and B and *Synedra* B during spring months.

Mayfly Life Histories and Food Habits

Baetidae

Baetis

Baetis was abundant at all sites and was the dominant mayfly at Stauffer 1. Species studied include *Baetis tricaudatus* from the Bigoray River and *Baetis persecuta* from Stauffer Creek and Tay River (Table 4). Adults of two other species, *Baetis brunneicolor* and *Baetis parvus*, were reared from Stauffer Creek. Both these species were obtained from Stauffer 2 while *Baetis brunneicolor* occurred only at Stauffer 1. I

Table 4. Mayfly species included in food habits study. Presence indicated by X.

	OCCURRENCE OF POPULATIONS			
	Stauf 1	Stauf 2	Tay	Bigoray
Ameletus sparsatus McDunnough			X	
Baetis spp.	X	X		
Baetis persecuta McDunnough			X	
Baetis tricaudatus Dodds				X
Caenis simulans McDunnough				X
Callibaetis coloradensis Banks				X
Centroptilum sp.		X		
Centroptilum spp.			X	X
Cinygmula mimus (Eaton)	X	X	X	
Epeorus sp.			X	
Ephemera simulans Walker		X		X
Ephemerella flavilinea McDunnough			X	
Ephemerella inermis Eaton	X	X	X	
Ephemerella spinifera Needham	X	X	X	
Ephemerella tibialis McDunnough	X	X	X	
Leptophlebia sp.		X		
Leptophlebia cupida (Say)				X
Paraleptophlebia sp.			X	
Paraleptophlebia debilis (Walker)		X		X
Pseudocloeon sp.			X	
Rhithrogena sp.			X	
Siphlonurus alternatus (Say)				X
Siphloplecton basale (Walker)				X
Stenacron canadense (Walker)				X

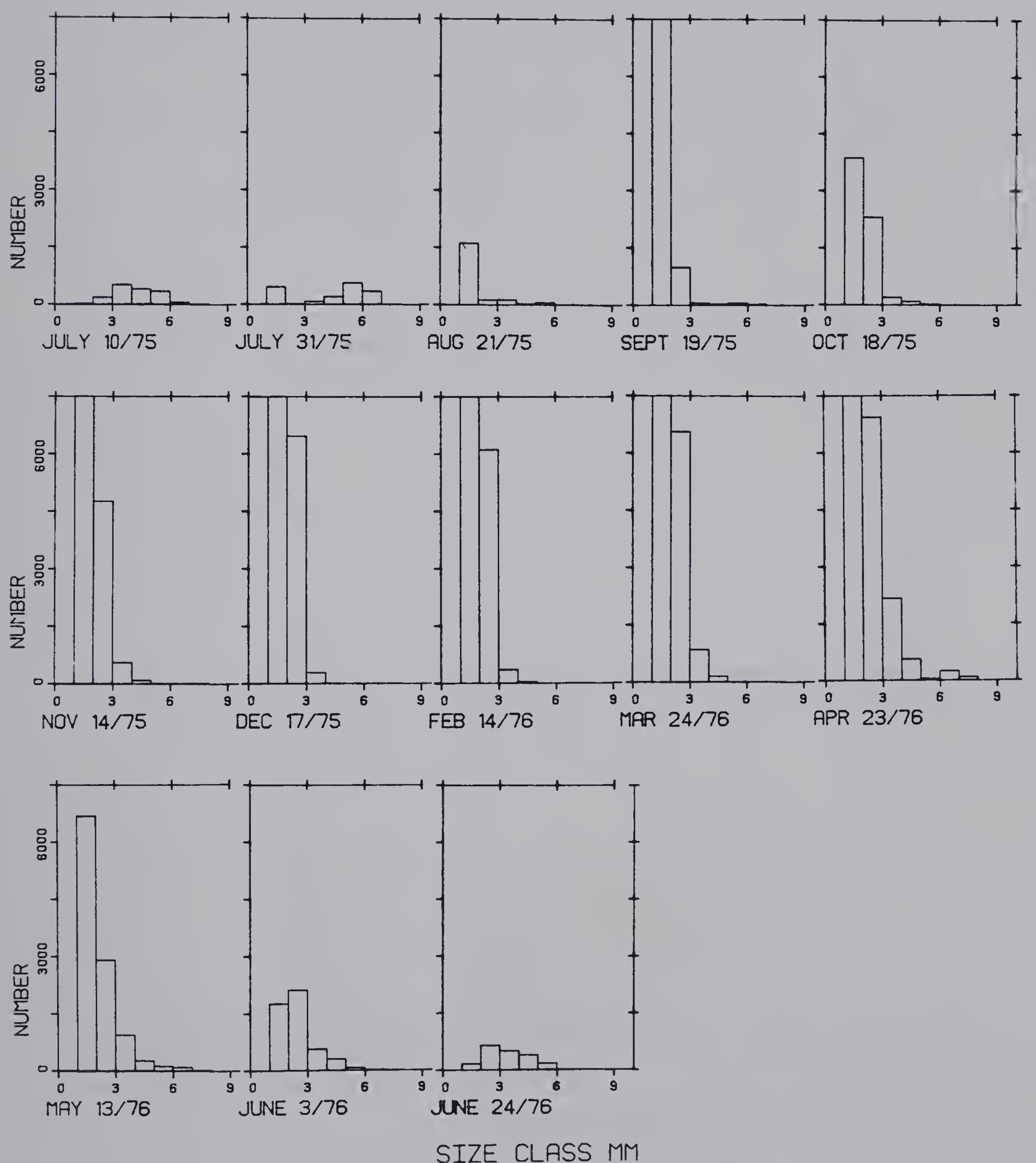

Figure 10. Number of Baetis spp. nymphs per mm size class, Stauffer 1.

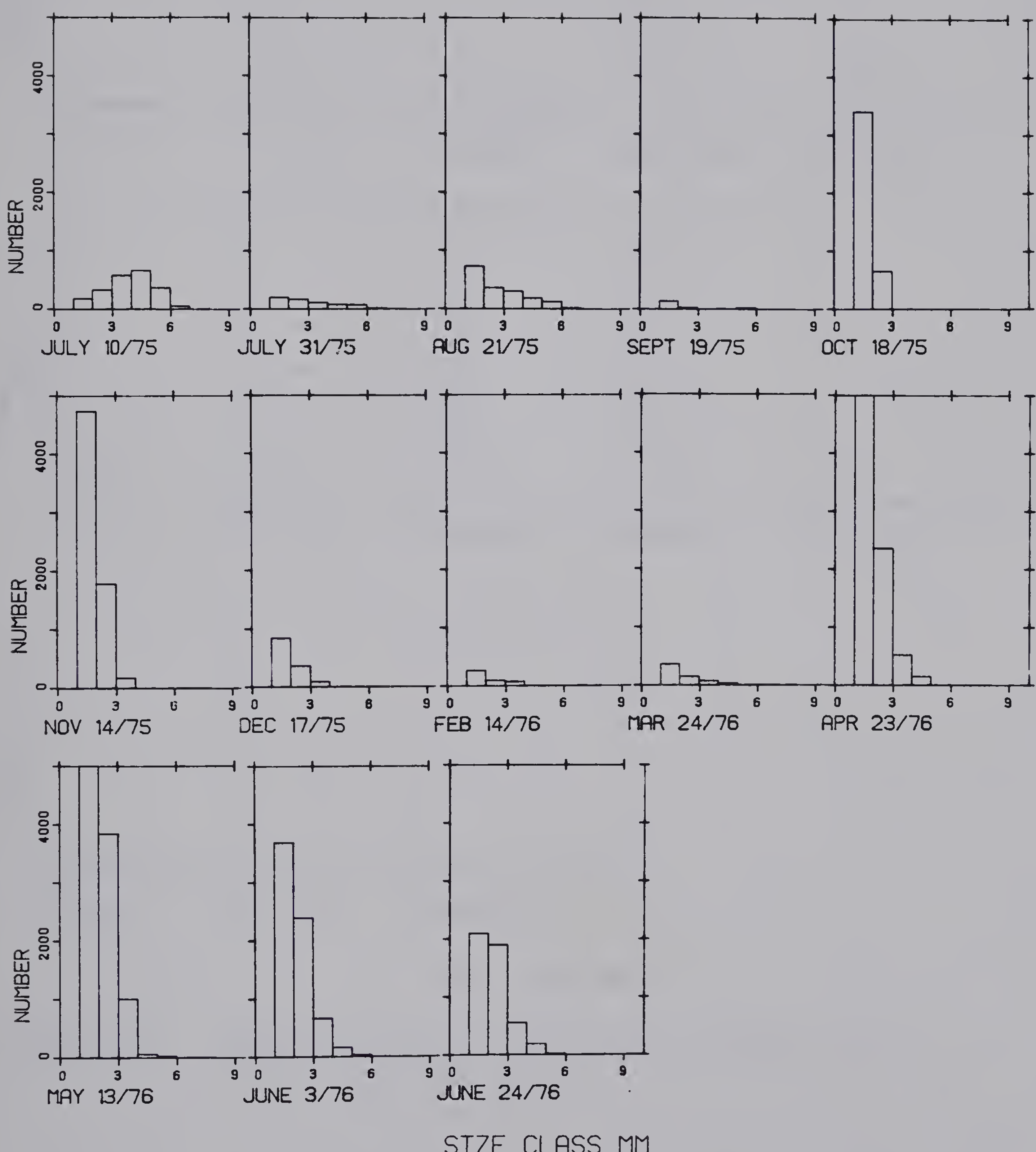

Figure 11. Number of Baetis spp. nymphs per mm size class, Stauffer 2.

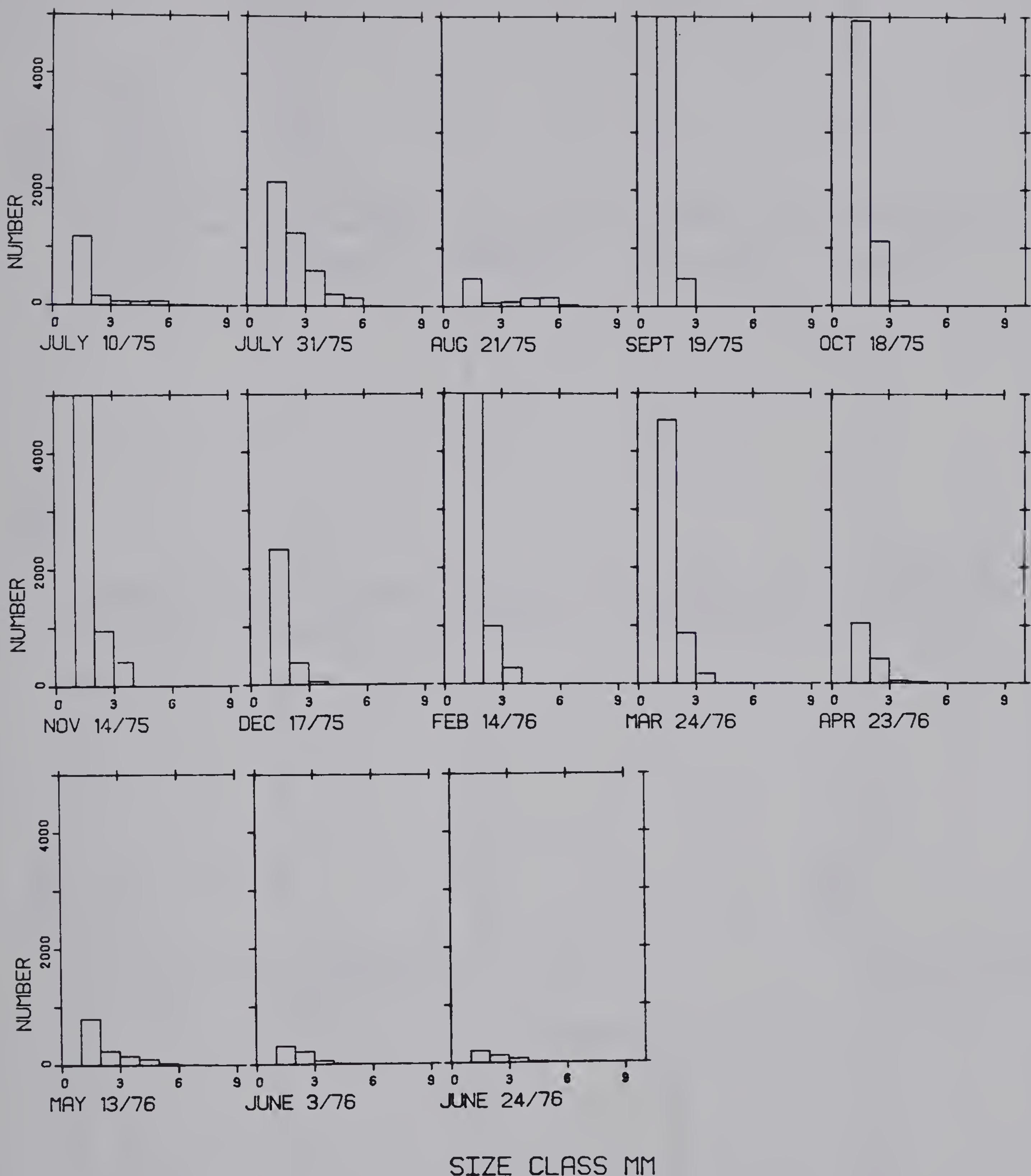

Figure 12. Number of <u>Baetis persecuta</u> nymphs per mm size class, Tay River.

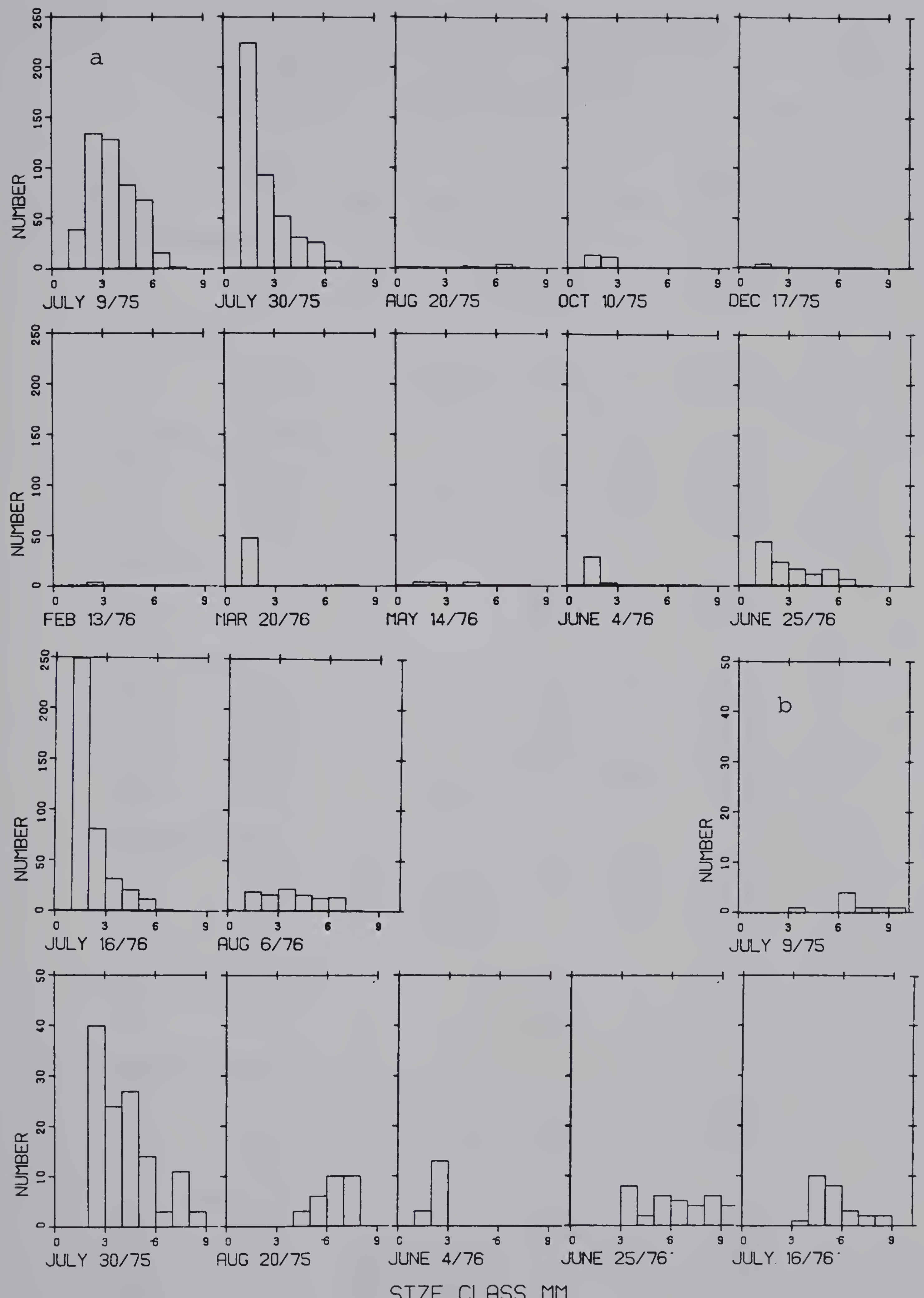

Figure 13. Number of <u>Baetis tricaudatus</u> nymphs per mm size class, Bigoray River (a); <u>Centroptilum</u> sp., Bigoray River (b).

Table 5. Average total volume of all ingested material per nymph and percent of total volume composed of detritus, Bigoray River, 1975 and 1976.

Species and Size Class	Average Total Volume ($um^3 x 10^6$)	JFM	AMJ	JAS	OND	Percent Volume Detritus
Baetis tricaudatus						
2-4	9.2			9.2		85.6
4-6	42.0		36.8	43.4		74.1
6-8	92.6		75.1	97.0		81.8
8-10	87.9			87.9		54.9
Caenis simulans						
2-4	8.4		10.7	6.1		94.4
4-6	41.7		47.1	37.5		95.2
6-8	109.6		109.6			96.4
Callibaetis coloradensis						
2-4	9.6			10.2	7.6	85.3
4-6	44.4		48.3	47.0	23.6	87.8
6-8	129.0		120.0	143.9	87.0	87.8
8-10	166.6		205.0		172.0	95.2
10-12	431.5		431.5			95.5
Centroptilum spp.						
2-4	29.9			29.9		-
4-6	59.2			59.2		86.2
6-8	85.2			85.2		84.1
8-10	176.0			176.0		87.5
Ephemera simulans						
2-4	8.0	5.9	12.5	5.9	6.2	96.8
4-6	44.1		35.7	69.5		95.3
6-8	101.6			101.6		92.4
8-10	190.0		166.0	202.0		95.7
10-12	331.5			331.5		91.0
12-14	1412.0			1651.0	695.0	95.2
14-16	929.5			729.0	1130.0	95.2
20-21	1490.0		1490.0			96.8
Leptophlebia cupida						
2-4	18.1	33.6		12.8	18.3	96.0
4-6	70.9	65.3	90.1	67.3	70.8	95.7
6-8	208.5	205.0	296.3		160.0	96.5
8-10	349.2	419.5	402.0		152.0	96.8
10-12	536.6	903.0	489.0			96.4
12-14	979.0		979.0			97.9
Paraleptophlebia debilis						
2-4	25.9			25.9		95.1
4-6	102.0			102.0		95.9
6-8	129.7			129.7		95.5
Siphlonurus alternatus						
2-4	13.5		13.5			95.1
4-6	73.3		73.3			92.8
6-8	326.0		239.5	499.0		96.9
8-10	414.3		426.0	408.0		97.7
10-12	792.9		779.7	836.0		97.7
12-14	800.0		800.0			98.3
Siphloplecton basale						
8-10	338.0			338.0		94.0
10-12	619.5	645.0		594.0		94.5
12-14	878.0	1130.0	862.5		731.0	95.6
14-16	976.2	987.5	1016.0			95.8
16-18	926.3	1040.0	869.5			96.8
Stenacron canadense						
6-8	194.0		194.0			95.6
8-10	312.0		374.0	250.0		97.4

Table 6. Average total volume of all ingested material per nymph and percent of total volume composed of detritus, Stauffer 1, 1975 and 1976.

Species and Size Class	Average Total Volume ($\mu m^3 \times 10^6$)	JFM	AMJ	JAS	OND	Percent Volume Detritus
Baetis spp.						
2-4	11.1	10.6	12.2	10.4	10.9	79.3
4-6	38.5	27.6	49.4	38.2	28.3	79.3
6-8	59.4		38.5	64.6		72.4
Cinygmula mimus						
2-4	13.0	9.8	21.2		8.0	78.4
4-6	49.1	33.8	52.7	74.1	49.7	79.1
6-8	96.9		109.6	71.7		69.0
8-10	178.3		259.0	97.6		52.6
Ephemerella inermis						
2-4	22.2				22.2	89.3
4-6	60.5	68.6			56.4	88.8
6-8	149.6	93.7	205.5			90.0
8-10	322.3	112.0	392.3			93.7
Ephemerella spinifera						
6-8	114.0				114.0	95.9
8-10	149.0	149.0				96.8
10-12	440.0	334.0	546.0			96.8
12-14	639.0		639.0			95.5
Ephemerella tibialis						
4-6	74.8			74.8		88.3
6-8	165.0			170.3	149.0	85.4

Table 7. Average total volume of all ingested material per nymph and percent of total volume composed of detritus, Stauffer 2, 1975 and 1976.

Species and Size Class	Average Total Volume ($um^3 x 10^6$)	JFM	AMJ	JAS	OND	Percent Volume Detritus
Baetis spp.						
2-4	15.1	12.8	14.7	9.0	5.6	83.3
4-6	34.8	22.6	39.6	27.0		82.7
6-8	68.1			68.1		45.4
Centroptilum sp.						
2-4	27.0			27.0		82.3
4-6	38.0			37.9		83.7
6-8	97.9			97.9		85.4
8-10	129.0			129.0		86.5
Cinygmula mimus						
2-4	18.7	20.4	17.9			93.1
4-6	63.3		61.9	69.1		92.2
6-8	131.9		149.3	69.8		91.9
8-10	176.0		176.0			93.1
Ephemera simulans						
2-4	8.0		8.5	8.0	7.6	95.1
4-6	35.4			35.4		95.1
6-8	89.1		100.0	78.2		95.9
8-10	154.5		205.0	137.7		95.4
10-12	291.7		271.8	355.0	236.0	97.2
12-14	596.3		583.7	501.7	703.7	96.6
14-16	919.9		940.0	894.0	849.0	96.9
16-18	1384.7		948.0	1370.0	1410.0	96.8
Ephemerella inermis						
2-4	10.9	9.2	15.1		7.8	93.9
4-6	53.3	44.9	72.5	47.4	35.2	92.1
6-8	142.9	66.6	196.0	59.0		96.1
Ephemerella spinifera						
2-4	30.4			30.4		84.4
4-6	118.0			118.0		90.6
8-10	217.6	155.0	103.0		276.7	93.7
10-12	386.0		386.0			99.4
12-14	591.0		591.0			99.0
Leptophlebia cupida						
2-4	26.3	33.4		18.5	38.5	95.4
4-6	53.0	59.5		45.7	51.1	92.9
6-8	83.0	89.5			76.5	91.2
Paraleptophlebia debilis						
2-4	17.1			11.3	28.6	96.0
4-6	70.4	60.5	101.7	74.9	51.5	95.4
6-8	83.0	89.5			76.5	96.5

Table 8. Average total volume of all ingested material per nymph and percent of total volume composed of detritus, Tay River, 1975 and 1976.

Species and Size Class	Average Total Volume ($um^3 x 10^6$)	JFM	AMJ	JAS	OND	Percent Volume Detritus
Ameletus sparsatus						
4-6	35.3	35.3				94.8
6-8	60.6	77.9			43.3	96.2
8-10	192.2	184.5			127.5	93.8
10-12	364.0	364.0			197.3	95.8
12-14	277.0	277.0				94.9
Baetis persecuta						
2-4	8.3	7.8	8.8	9.6	6.0	85.6
4-6	33.6		27.2	41.1		82.2
6-8	58.1		41.6	63.5		91.0
Cinygmula mimus						
2-4	19.1	16.0	18.1	34.8	11.9	88.4
4-6	48.9	40.2	50.6	42.3	57.0	83.6
6-8	109.6	161.5	105.4	89.7	85.8	86.5
Epeorus sp.						
2-4	16.4		16.4			88.6
4-6	36.5		42.6	30.3		79.7
6-8	80.3		87.1	73.5		80.8
8-10	174.0			174.0		85.3
Ephemerella flavilinea						
2-4	14.9		14.9			85.1
4-6	49.8		49.8			94.4
6-8	111.0		111.0	111.0		94.2
8-10	137.0			137.0		97.9
Ephemerella inermis						
2-4	13.4	13.4				97.3
4-6	26.9		31.3	18.2		96.7
6-8	73.0		66.0	79.9		88.4
Ephemerella spinifera						
4-6	96.6			96.6		78.2
6-8	175.0				175.0	69.9
8-10	210.0				210.0	66.9
10-12	299.0		299.0			-
12-14	671.0		671.0			91.6
Ephemerella tibialis						
2-4	21.1			21.1		95.5
4-6	90.0			90.0		96.8
6-8	246.0			246.0		98.3
Paraleptophlebia sp.						
2-4	13.9	14.7		15.8	10.1	96.6
4-6	51.3	60.9	90.6	30.0	33.0	94.4
6-8	86.7	113.0	81.1		38.5	95.0
Rhithrogena sp.						
4-6	62.3			45.2	79.4	84.1
6-8	129.2	175.5	112.0		103.9	87.1
8-10	209.0				209.0	92.5
Pseudocloeon sp.						
2-4	9.5		9.1		10.0	
4-6	31.4				31.4	

could not distinguish the nymphs of *B. persecuta*, *B. brunneicolor* and *B. parvus*; however most of the Stauffer Creek adults collected and reared were *B. persecuta*, and I believe most of the nymphs studied were *B. persecuta*.

The life history of *Baetis* spp. at all sites was characterized by hatching of eggs and rapid growth during the late summer and autumn (Fig. 10, 11, 12, 13a). Delayed hatching appeared to occur throughout the winter, along with a reduced growth rate. Rate of growth increased in the spring and emergence took place in late spring and summer. An influx of small nymphs during late June at both Stauffer Creek sites and during early July at the Tay and Bigoray Rivers could be due to a second rapid summer generation (Clifford 1969). At Stauffer Creek, the second generation could represent appearance of one of the two additional species.

The major food item ingested by all *Baetis* spp. nymphs was detritus, with diatoms ranking second (Tables 5, 6, 7, 8). Filamentous algae was insignificant in the diet of *Baetis* from all sites, never composing more than 0.1% of material consumed. At Stauffer 1, filamentous algae were recorded once in December; at Stauffer 2 and Bigoray River these algae were detected on odd occasions throughout the year. *Baetis*

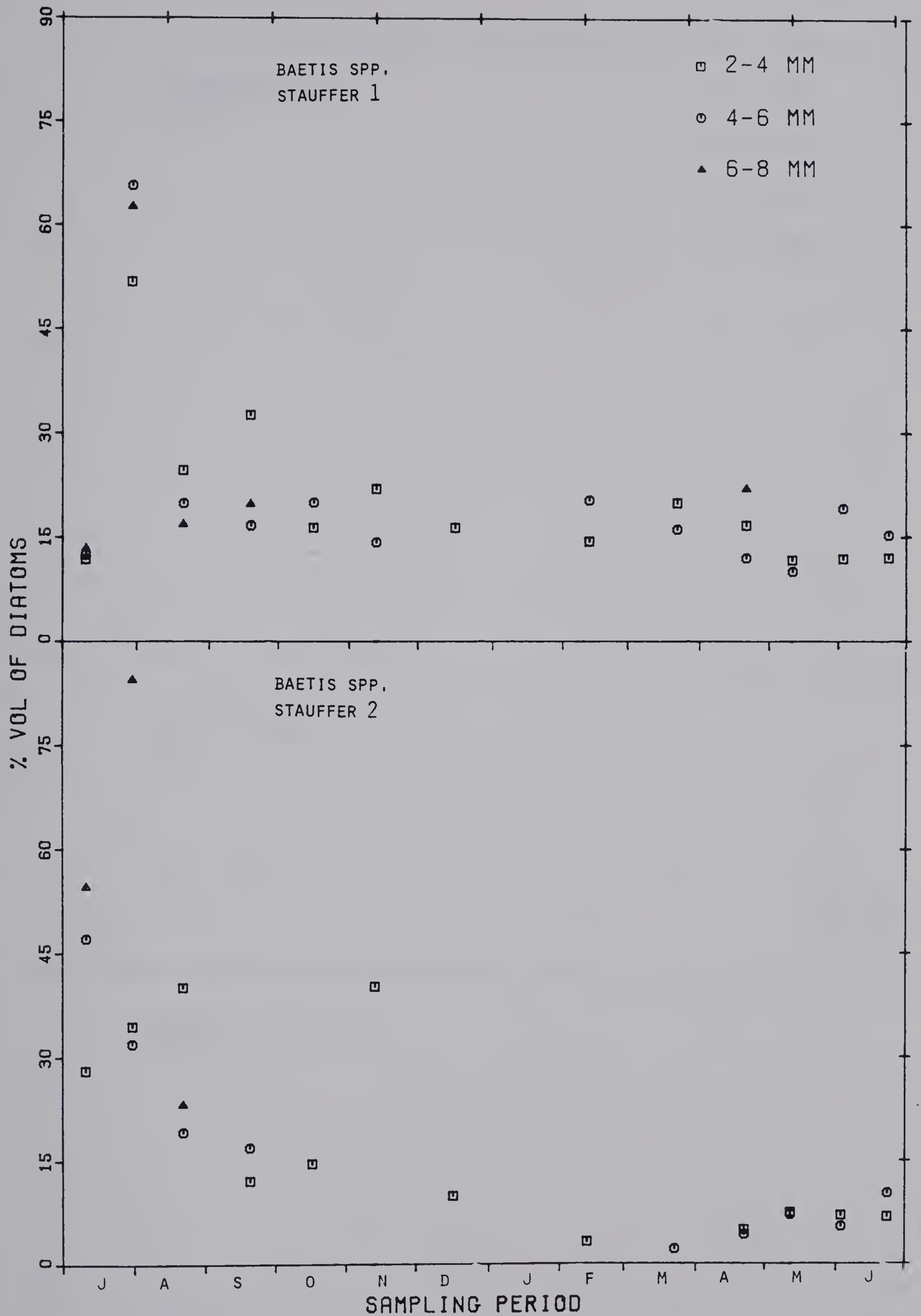

Figure 14. Proportion of ingested material composed of diatoms for the various size classes of <u>Baetis</u> spp. nymphs, Stauffer 2. (1975-1976).

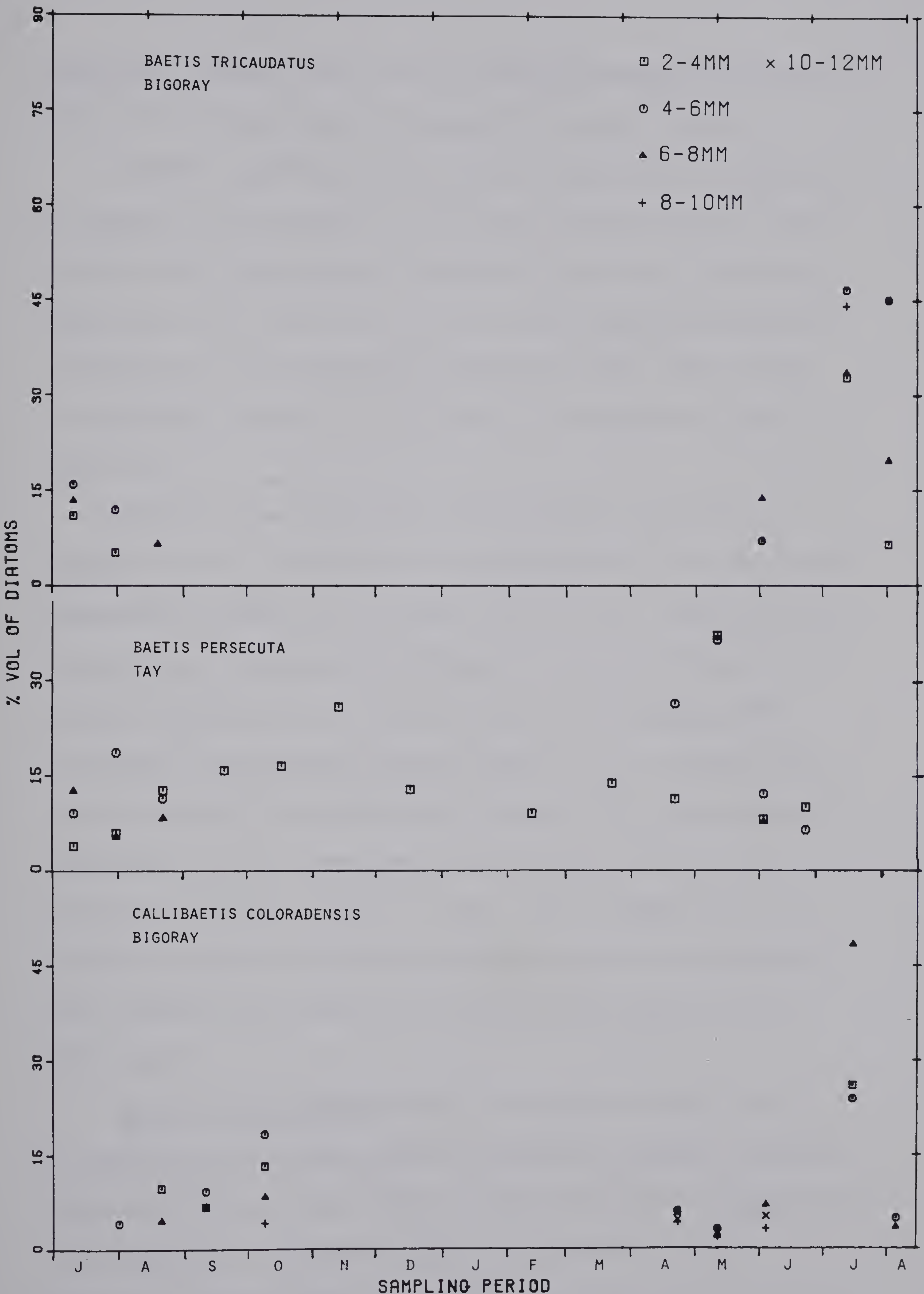

Figure 15. Proportion of ingested material composed of diatoms for the various size classes of <u>Baetis tricaudatus</u> nymphs from Bigoray River, <u>B. persecuta</u> from Tay River, <u>Callibaetis coloradensis</u> from Bigoray River. (1975 and 1976).

persecuta nymphs from the Tay River ingested filamentous algae most often during spring and summer months.

Mineral particles were also a minor diet component of *Baetis*. At Stauffer 1, Bigoray and Tay Rivers, sand grains were consistently found in the guts, but they comprised less than 1% of the total volume of material ingested on most occasions (maximum 2.3%). The range at Stauffer 2 was 0.1-1.8% with an average of less than 1%.

The detrital component of ingested material of Tables 5, 6, 7, 8 is the average proportion of detritus ingested by each 2 mm nymphal size class. Since mineral material and filamentous algae were insignificant, and animal fragments were never observed in *Baetis* spp. stomachs, the consumption of detritus can essentially be considered the difference between the proportion of ingested material composed of diatoms and the total material consumed (Fig. 14, 15). An increase in the percent volume of diatoms consumed can be interpreted as a relative decrease in detrital consumption, and vice versa.

Baetis tricaudatus from the Bigoray River and *B. persecuta* from Tay River generally consumed greater than 80% detritus and often greater than 85%. *Baetis* spp. from Stauffer 1 usually ingested from 75% to 85% detritus. Nymphs from Stauffer 2 had the most variable

detrital ingestion rates, fluctuating between 55% and 95%.

Baetis nymphs from Stauffer 1 had peak seasonal diatom consumption (maximum 65%) in late July. Diatom ingestion by *Baetis* nymphs from Stauffer 2 was different from the upstream site due to a second peak in diatom consumption in late autumn (maximum 40%). During winter, diatom ingestion was lower (therefore detrital ingestion higher) at Stauffer 2 compared to Stauffer 1. Epilithic standing crops at Stauffer 2 correlated well with diatom consumption, high summer densities preceding an autumn peak in consumption. In contrast, Stauffer 1 epilithic densities did not coincide as closely with diatom ingestion patterns, e.g. maximum rates of diatom consumption in late July preceded the September-October peak of epilithic standing crops. At both sites epilithic populations were relatively uniform during winter, with a decline in spring. Large nymphs collected at both Stauffer 1 and 2 often consumed higher than average proportions of diatoms compared to smaller size nymphs.

Baetis persecuta nymphs in the Tay River ingested about 10% diatoms throughout most of the study period, with one peak near 25% in autumn and a spring peak (maximum 37%) in May. There were no clear size class trends.

Table 9. Average total ingested volume for all mayfly species.

Size Class	Average Total Volume ($\times 10^6$ um^3)	Range of Population Averages
2-4 mm	15.9	8.02 - 30.4
4-6	55.8	26.90 - 118.9
6-8	123.1	58.05 - 326.0
8-10	214.1	87.9 - 414.0
10-12	449.1	291.0 - 792.0
12-14	685.8	277.0 - 1412.0
14-16	941.4	919.0 - 976.2
16-18	1155.5	926.3 - 1384.7
20-22	1490.0	

Unfortunately insufficient specimens of *B. tricaudatus* from the Bigoray River were available during autumn and winter for stomach analyses. Detrital ingestion by Bigoray *Baetis* was very high during summer 1975 and spring 1976; however during July and August 1976, a sharp increase in relative diatom ingestion occurred (maximum 47%) for some nymphal size classes.

Seasonal epilithic standing crop peaks from Bigoray and Tay Rivers correlate well with seasonal diatom consumption rates of the *Baetis* nymphs of these streams. Spring and autumn peaks of both diatom standing crop and ingestion occurred in Tay River, in contrast to a single early summer peak in the Bigoray River.

Total volume of material consumed for all *Baetis* spp. size classes from all sites (Tables 5, 6, 7, 8) was below the study average (Table 9). Seasonally, the 2-4 mm and 4-6 mm *Baetis* nymphs at both Stauffer sites consumed the greatest quantity of food items during spring (AMJ). Similar size nymphs of the Tay and Bigoray Rivers ingested peak quantities of material in summer (JAS), as did 6-8 mm specimens from all sites.

The size distribution of ingested particles analyzed (up to 161 um diameter) was divided into four

Table 10. Size class averages of percent material consumed in each particle size class (PSC) range. Bigoray River (1975-1976).

Species	Size Class	PSCI <32um	PSCII 32-64um	PSCIII 64-101um	PSCIV 101-161um
Baetis tricaudatus	2-4	74	18	6	2
	4-6	72	20	6	2
	6-8	76	18	5	1
	8-10	72	18	6	4
Caenis simulans	2-4	65	27	7	1
	4-6	61	28	9	2
	6-8	52	30	13	5
Callibaetis coloradensis	2-4	66	20	10	4
	4-6	71	22	5	2
	6-8	68	23	5	4
	8-10	65	25	8	2
	10-12	62	27	10	1
Centroptilum spp.	2-4	77	7	4	13
	4-6	72	19	4	5
	6-8	72	21	6	1
	8-10	64	23	9	4
Ephemera simulans	2-4	71	18	8	3
	4-6	74	19	4	3
	6-8	72	20	7	1
	8-10	67	22	10	1
	10-12	61	24	14	1
	12-14	61	23	11	5
	14-16	60	23	10	7
	20-21	68	25	6	1
Leptophlebia cupida	2-4	63	25	9	3
	4-6	59	26	10	5
	6-8	57	28	11	4
	8-10	58	29	10	3
	10-12	49	27	14	10
	12-14	49	27	16	8
Paraleptophlebia debilis	2-4	71	21	4	5
	4-6	61	26	11	2
	6-8	68	20	8	4
Siphlonurus alternatus	2-4	75	20	4	1
	4-6	70	23	8	0
	6-8	55	25	17	3
	8-10	55	26	14	5
	10-12	52	26	15	7
	12-14	50	25	16	9
Siphloplecton basale	8-10	58	24	16	2
	10-12	56	27	11	6
	12-14	61	25	9	5
	14-16	60	27	8	5
	16-18	62	26	9	3
Stenacron canadense	6-8	61	26	11	2
	8-10	67	23	8	2

Table 11. Size class averages of percent material consumed in each particle size class (PSC) range. Stauffer 1 and Stauffer 2 (1975-1976).

Species	Size Class	PSCI <32um	PSCII 32-64um	PSCIII 64-101um	PSCIV 101-161um
Stauffer 1					
Baetis spp.	2-4	67	25	6	2
	4-6	62	29	7	2
	6-8	61	28	8	3
Cinygmula mimus	2-4	72	19	7	2
	4-6	69	22	7	2
	6-8	64	27	8	1
	8-10	69	24	5	2
Ephemerella inermis	2-4	58	29	9	5
	4-6	54	30	12	4
	6-8	47	31	17	5
	8-10	42	29	20	9
Ephemerella spinifera	6-8	34	32	29	5
	8-10	29	19	22	30
	10-12	40	22	17	21
	12-14	36	23	18	24
Ephemerella tibialis	4-6	56	28	13	3
	6-8	52	28	16	4
Stauffer 2					
Baetis spp.	2-4	70	19	6	5
	4-6	80	15	4	1
	6-8	82	12	4	2
Centroptilum	2-4	77	15	6	1
	4-6	81	15	3	1
	6-8	79	18	3	0
	8-10	74	21	5	0
Cinygmula mimus	2-4	81	16	3	0
	4-6	77	16	5	2
	6-8	80	13	5	2
	8-10	74	16	7	3
Ephemera simulans	2-4	71	17	8	4
	4-6	72	19	6	3
	6-8	63	21	10	6
	8-10	70	21	7	2
	10-12	66	23	8	3
	12-14	68	22	8	2
	14-16	64	23	9	4
	16-18	63	25	9	3
Ephemerella inermis	2-4	69	22	7	2
	4-6	60	26	10	4
	6-8	55	28	12	5
Ephemerella spinifera	2-4	59	24	13	4
	4-6	68	24	8	0
	8-10	47	23	17	13
	10-12	37	18	21	24
	12-14	36	17	20	27
Leptophlebia sp.	2-4	66	23	9	2
	4-6	67	24	8	1
	6-8	64	24	9	3
Paraleptophlebia debilis	2-4	68	20	7	5
	4-6	69	22	7	2
	6-8	71	21	6	2

Table 12. Size class averages of percent material consumed in each particle size class (PSC) range. Tay (1975-1976).

Species	Size Class	PSCI <32um	PSCII 32-64um	PSCIII 64-101um	PSCIV 101-161um
Ameletus sparsatus	4-6	65	23	10	2
	6-8	64	25	10	1
	8-10	60	24	11	5
	10-12	55	25	15	6
	12-14	66	20	9	5
Baetis persecuta	2-4	74	17	6	3
	4-6	75	17	5	3
	6-8	73	20	6	1
Cinygmula mimus	2-4	71	15	7	7
	4-6	75	16	5	4
	6-8	71	19	7	3
Epeorus sp.	2-4	80	11	6	3
	4-6	83	12	3	2
	6-8	76	16	5	3
	8-10	76	17	4	2
Ephemerella flavilinea	2-4	72	17	7	4
	4-6	60	21	12	7
	6-8	58	26	11	5
	8-10	51	27	16	6
Ephemerella inermis	2-4	67	24	7	2
	4-6	60	21	11	8
	6-8	58	25	11	6
Ephemerella spinifera	4-6	59	20	14	8
	6-8	66	24	9	1
	8-10	64	21	11	4
	10-12	51	24	18	7
	12-14	44	26	15	16
Ephemerella tibialis	2-4	64	21	9	6
	4-6	65	24	7	5
	6-8	55	27	13	5
Paraleptophlebia sp.	2-4	70	20	7	3
	4-6	69	22	7	2
	6-8	72	19	7	2
Pseudocloeon sp.	2-4	72	18	8	2
	4-6	56	17	9	18
Rhithrogena sp.	4-6	74	18	5	3
	6-8	73	19	6	2
	8-10	61	24	10	6
$\bar{X}$		72	19	6	3

Table 13. Quarterly averages of percent material consumed in each particle size class (PSC) range, Bigoray River.(1975-1976).

Species	Season	PSCI <32um	PSCII 32-64um	PSCIII 64-101um	PSCIV 101-161um
Baetis tricaudatus	JAS	74	19	5	2
	OND	-	-	-	-
	JFM	-	-	-	-
	AMJ	71	21	7	1
	Yearly $\bar{X}$	73.6	19.3	5.3	1.9
Caenis simulans	JAS	61	29	8	2
	OND	-	-	-	-
	JFM	-	-	-	-
	AMJ	60	28	10	2
	Yearly $\bar{X}$	60.5	28.5	2.1	2
Callibaetis coloradensis	JAS	67	22	7	4
	OND	67	24	6	3
	JFM	-	-	-	-
	AMJ	68	24	7	1
	Yearly $\bar{X}$	67.3	23.3	6.6	2.7
Centroptilum spp.	JAS	71	19	6	4
	OND	-	-	-	-
	JFM	-	-	-	-
	AMJ	-	-	-	-
	Yearly $\bar{X}$	71	19	6	4
Ephemera simulans	JAS	64	22	11	3
	OND	68	22	8	2
	JFM	69	15	11	5
	AMJ	74	20	5	2
	Yearly $\bar{X}$	67.6	21.2	8.8	2.6
Leptophlebia cupida	JAS	67	24	7	2
	OND	56	27	12	5
	JFM	57	24	10	6
	AMJ	56	28	11	5
	Yearly $\bar{X}$	57.3	27.2	10.6	4.9
Paraleptophlebia debilis	JAS	66	22	9	3
	OND	-	-	-	-
	JFM	-	-	-	-
	AMJ	-	-	-	-
	Yearly $\bar{X}$	66	22	9	3
Siphlonurus alternatus	JAS	49	26	17	8
	OND	-	-	-	-
	JFM	-	-	-	-
	AMJ	60	24	12	4
	Yearly $\bar{X}$	56.8	24.6	13.5	5.2
Siphloplecton basale	JAS	56	25	14	5
	OND	57	24	12	7
	JFM	58	28	10	4
	AMJ	63	26	8	3
	Yearly $\bar{X}$	60.2	26.4	9.6	3.8
Stenacron canadense	JAS	72	21	6	1
	OND	-	-	-	-
	JFM	-	-	-	-
	AMJ	59	27	13	1
	Yearly $\bar{X}$	65.5	24	9.5	1

Table 14. Quarterly averages of percent material consumed in each particle size class (PSC) range, Stauffer 1 (1975-1976).

Species	Season	PSCI <32um	PSCII 32-64um	PSCII 64-101um	PSCIV 101-161um
Baetis spp.	JAS	68	24	6	2
	OND	73	22	4	1
	JFM	64	28	6	2
	AMJ	55	33	10	2
	Yearly $\overline{X}$	64.4	26.9	6.9	1.8
Cinygmula mimus	JAS	75	17	5	3
	OND	78	15	5	2
	JFM	75	16	6	3
	AMJ	61	28	9	2
	Yearly $\overline{X}$	68.4	22.1	7.2	2.4
Ephemerella inermis	JAS	-	-	-	-
	OND	56	29	11	4
	JFM	55	29	12	4
	AMJ	38	31	23	8
	Yearly $\overline{X}$	48.2	29.3	16.3	5.7
Ephemerella spinifera	JAS	-	-	-	-
	OND	34	32	29	5
	JFM	41	20	18	21
	AMJ	32	23	19	26
	Yearly $\overline{X}$	36	23.6	20.6	19.8
Ephemerella tibialis	JAS	53	28	15	4
	OND	58	31	8	3
	JFM	-	-	-	-
	AMJ	-	-	-	-
	Yearly $\overline{X}$	53.7	28.4	14	3.9

Table 15. Quarterly averages of percent material consumed in each particle size class (PSC) range. Stauffer 2 (1975-1976).

Species	Season	PSCI <32um	PSCII 32-64um	PSCIII 64-101um	PSCIV 101-161um
Baetis spp.	JAS	81	13	4	2
	OND	67	16	7	10
	JFM	83	13	3	1
	AMJ	70	22	6	2
	Yearly $\overline{X}$	76.3	16.1	4.8	2.8
Centroptilum sp.	JAS	78	17	4	1
	OND	-	-	-	-
	JFM	-	-	-	-
	AMJ	-	-	-	-
	Yearly $\overline{X}$	78	17	4	1
Cinygmula mimus	JAS	74	14	7	5
	OND	-	-	-	-
	JFM	83	16	2	0
	AMJ	79	15	5	1
	Yearly $\overline{X}$	78.5	14.9	5.1	1.5
Ephemera simulans	JAS	68	22	7	3
	OND	66	22	9	3
	JFM	-	-	-	-
	AMJ	65	22	9	4
	Yearly $\overline{X}$	66.4	22	8.3	3.3
Ephemerella inermis	JAS	62	26	10	2
	OND	68	22	8	2
	JFM	71	19	7	3
	AMJ	55	30	12	3
	Yearly $\overline{X}$	62.5	25.2	9.7	2.7
Ephemerella spinifera	JAS	64	24	10	2
	OND	51	25	16	8
	JFM	47	22	19	12
	AMJ	35	19	20	26
	Yearly $\overline{X}$	48.1	22.4	16.3	13.1
Leptophlebia sp.	JAS	67	21	9	3
	OND	63	25	9	3
	JFM	68	24	7	1
	AMJ	-	-	-	-
	Yearly $\overline{X}$	65.6	23.8	8.3	2.3
Paraleptophlebia debilis	JAS	68	22	8	2
	OND	67	23	6	4
	JFM	78	16	4	2
	AMJ	63	26	9	2
	Yearly $\overline{X}$	69.5	21.3	6.7	2.5

Table 16. Quarterly averages of percent material consumed in each particle size class (PSC) range. Tay (1975-1976).

Species	Season	PSCI <32um	PSCII 32-64um	PSCIII 64-101um	PSCIV 101-161um
Ameletus sparsatus	JAS	-	-	-	-
	OND	60	25	11	4
	JFM	63	23	11	3
	AMJ	-	-	-	-
	Yearly $\bar{X}$	61.8	23.8	11	3.4
Baetis persecuta	JAS	73	20	5	2
	OND	76	18	5	1
	JFM	75	19	4	2
	AMJ	75	16	5	4
	Yearly $\bar{X}$	74.3	18.2	4.9	2.6
Cinygmula mimus	JAS	61	17	9	13
	OND	69	21	8	2
	JFM	75	14	6	5
	AMJ	78	15	5	2
	Yearly $\bar{X}$	72	16.7	6.7	4.6
Epeorus sp.	JAS	81	15	3	1
	OND	-	-	-	-
	JFM	-	-	-	-
	AMJ	78	13	5	4
	Yearly $\bar{X}$	79.3	13.8	4.2	2.8
Ephemerella flavilinea	JAS	52	27	13	8
	OND	-	-	-	-
	JFM	-	-	-	-
	AMJ	64	20	10	6
	Yearly $\bar{X}$	60.6	22	10.9	6.6
Ephemerella inermis	JAS	67	20	8	5
	OND	-	-	-	-
	JFM	67	24	7	2
	AMJ	54	24	13	9
	Yearly $\bar{X}$	60.5	22.7	10.3	6.5
Ephemerella spinifera	JAS	59	20	14	8
	OND	65	23	10	2
	JFM	-	-	-	-
	AMJ	48	25	16	11
	Yearly $\bar{X}$	57.3	22.7	13.3	7.0
Ephemerella tibialis	JAS	62	24	8	6
	OND	-	-	-	-
	JFM	-	-	-	-
	AMJ	-	-	-	-
	Yearly $\bar{X}$	62	24	8	6
Paraleptophlebia sp.	JAS	65	24	8	3
	OND	70	21	7	2
	JFM	69	20	7	4
	AMJ	80	14	4	2
	Yearly $\bar{X}$	69.9	20.4	6.8	2.9
Pseudocloeon sp.	JAS	65	17	8	10
	OND	-	-	-	-
	JFM	-	-	-	-
	AMJ	69	20	8	2
	Yearly $\bar{X}$	66.3	18	8	7.3
Rhithrogena sp.	JAS	72	17	6	6
	OND	68	21	7	4
	JFM	78	17	4	1
	AMJ	79	17	3	2
	Yearly $\bar{X}$	71.9	19.2	5.8	3.3

Table 17. Average particle size distribution for all mayfly species, from all sites.

Size of Particles	% of Total Consumed Volume	Range
PSC I (<32 um)	65.4	36.0 - 79.3
PSC II (32-64 um)	21.6	13.0 - 29.8
PSC III (64-101 um)	8.6	3.0 - 20.6
PSC IV (101-161 um)	4.4	0.0 - 19.8

particle size class (PSC) ranges. PSCI represents particles with diameters 32 um or less, PSCII particles have diameters of 32-64 um, PSCIII particles have diameters 64-101 um, and PSCIV particles have diameters 101-161 um. The proportion of the total volume of consumed material made up of particles in each PSC range was calculated, and the average proportion for each nymphal size class is reported in Tables 10, 11, 12. The seasonal distribution of particle sizes consumed by each species is reported in Tables 13, 14, 15, 16. These tables depict the average proportion of particles ingested in each PSC range during each quarter of the year.

The size of particles consumed by *Baetis* nymphs from Bigoray River, Tay River, and Stauffer 2 was generally smaller than average; i.e. the percentage of particles in PSCI was considerably greater than the study average (Table 17). *Baetis* nymphs from Stauffer 1 ingested above average proportions of PSCII particles, while PSCI particles were present in below average quantities in nymphs of this station.

No seasonal fluctuations in average particle sizes consumed occurred for *B. persecuta* nymphs from Tay River, except for elevated PSCI ingestion coincident with the May diatom peak. *Baetis tricaudatus* from Bigoray River consumed similar size particles throughout

the year, except for a slight trend towards smaller particles during summer.

An increased proportion of small particles were consumed by _Baetis_ nymphs during autumn at Stauffer 1, and this correlates with an increased diatom consumption at that time. Larger size particles accounted for high proportions of the total material consumed during spring months, when detrital ingestion was greatest. The highest relative ingestion of small particles by Stauffer 2 _Baetis_ occurred during late summer (JAS) and winter (JFM).

Most workers report _Baetis_ as being a combined diatom-detritus feeder. Some reports (Jones 1950, Brown 1961b, Chapman and Demory 1963, Gilpin and Brusven 1970, Shapas and Hilsenhoff 1976) indicate detritus as the most important component, whereas other workers (Percival and Whitehead 1929, Badcock 1949, Ivanova 1958, Minckley 1963) found _Baetis_ to be largely a diatom feeder. Moore (1977) reported two arctic species to be complete detritivores. Filamentous algae has generally not been detected as a major diet component of _Baetis_ nymphs. Crisp (1956) observed _Simulium_ larvae in _Baetis_ nymphs; however, to my knowledge, this is the only report of ingestion of animal material by nymphs of this genus. The contrasting results reported, particularly for relative frequency

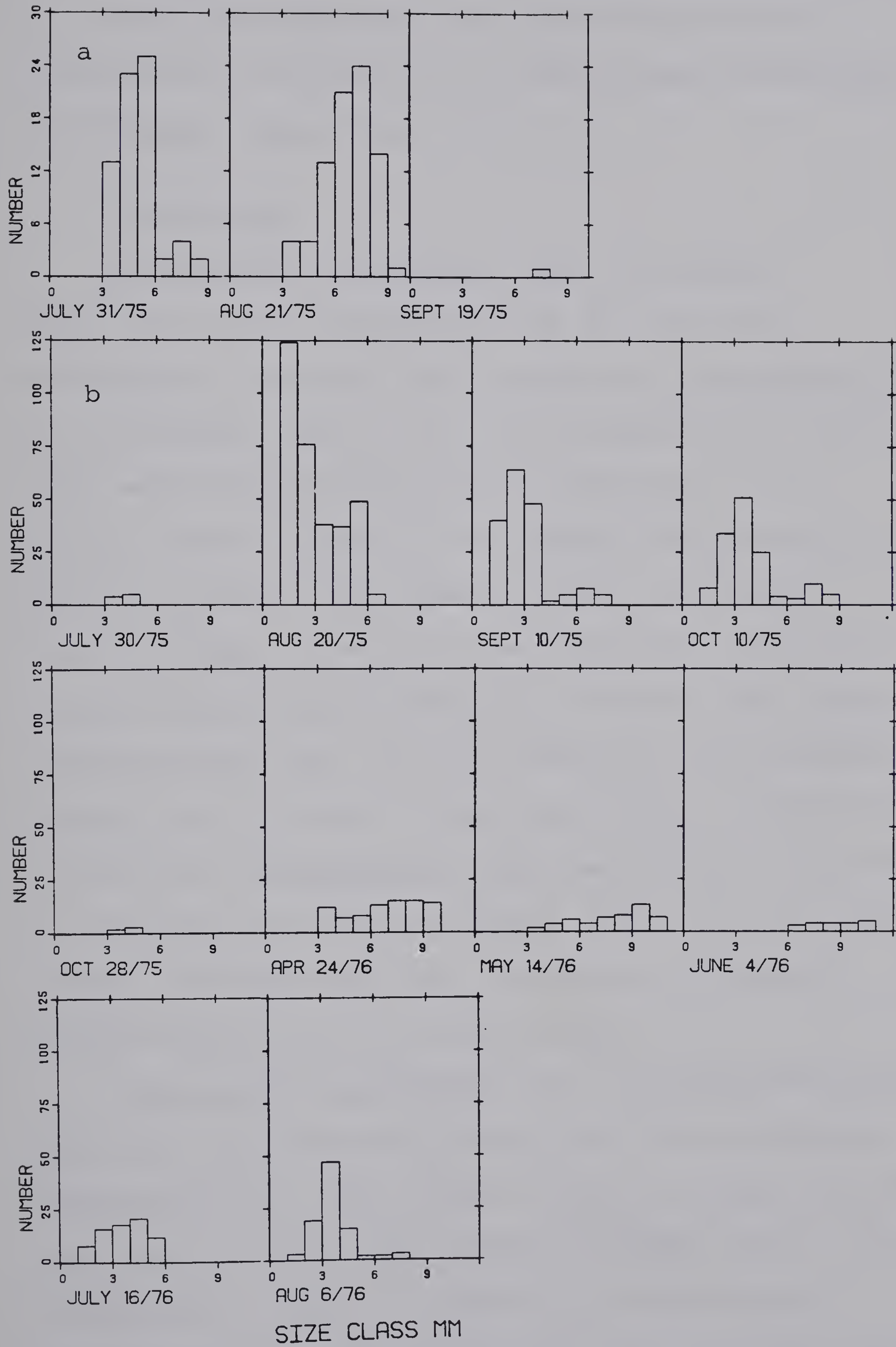

Figure 16. Number of <u>Centroptilum</u> sp. nymphs per mm size class, Stauffer 2 (a); <u>Callibaetis</u> <u>coloradensis</u>, Bigoray River (b).

of detritus and diatoms, are likely a function of differences in availability of various diet components at different seasons and sites.

Callibaetis

Callibaetis coloradensis from the Bigoray River was the only representative of this genus encountered. Clifford (1969) reports _C. coloradensis_ in the Bigoray River to be a univoltine winter species with rapid autumn growth and no growth during the winter. Growth resumes in the spring and emergence occurs throughout the summer. My data corroborate these findings, as well as the observation that this species occurs predominantly in backwaters and along stream margins (Fig. 16). No specimens were collected during winter because I could only sample in midstream-riffle sites; _Callibaetis_ nymphs were likely restricted to backwaters during this period. During the ice-free season, specimens were most often observed amongst the macrophytes of the stream margin.

Callibaetis coloradensis was a herbivore-detritivore with detritus averaging greater than 85% of material ingested for all size classes (Table 5). Nymphs greater than 8 mm in length consistently consumed greater than 95% detritus. Seasonally detrital consumption was greatest during spring months and least important during mid-summer.

Peak diatom consumption (48% maximum) occurred during July 1976, correlating with an epilithic diatom peak at that time. Diatom consumption was lowest during spring months and intermediate during September and October (Fig. 15). Size class trends indicate greater consumption of diatoms by smaller nymphs, particularly in autumn.

Filamentous algae were detected in *C. coloradensis* stomach samples during October and April but were less than 0.3% of the total food volume. Mineral particles generally accounted for 0.5-1.0% of the total stomach volume.

Total volume of material consumed was below average for all size classes except the 4-6 mm class. Seasonally, the highest volume of food consumed by *Callibaetis* nymphs was recorded during spring and summer with a reduction in food consumption for all size classes during autumn (OND).

Size of particles consumed by *C. coloradensis* was slightly above the study average for particles less than 64 um in diameter (PSCI). This pattern was most evident in small size class nymphs.

Most investigators report *Callibaetis* nymphs to be predominantly herbivorous, often ingesting epiphytic diatoms and filamentous algae (Morgan 1913, Berner 1950, Edmunds et.al. 1976). Trost and Berner (1963)

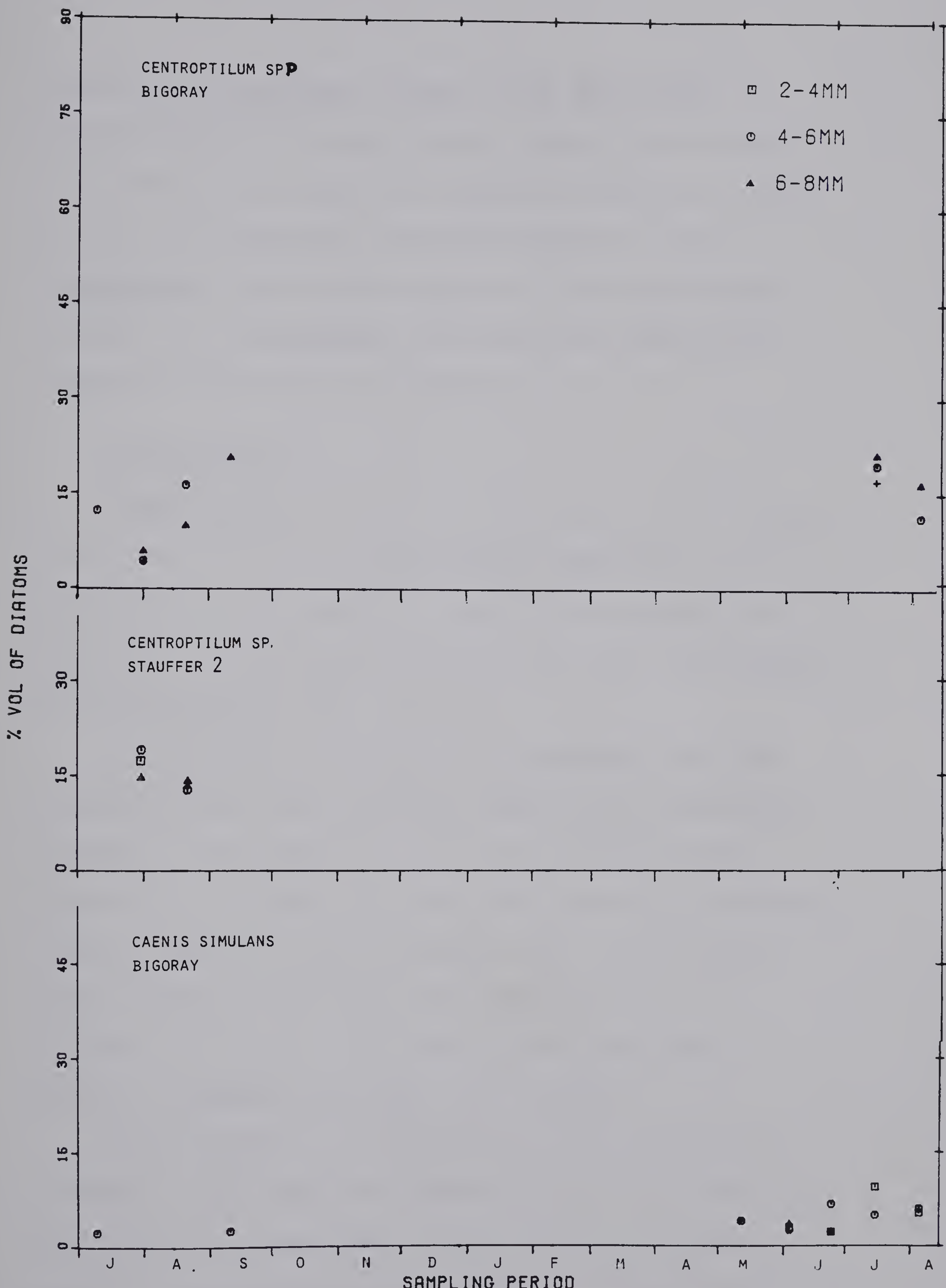

Figure 17. Proportion of ingested material composed of diatoms for the various size classes of Centroptilum spp. nymphs, Bigoray River, Centroptilum sp., Stauffer 2, Caenis simulans, Bigoray River. (1975-1976).

observed *C. floridanus* nymphs to be most often associated with vascular plants, however they report it as being a non-specific feeder on decaying leaves as well as filamentous algae and diatoms. The *C. coloradensis* populations appear to have food habits similar to *C. floridanus*, with detritus being most important except during mid-July.

Centroptilum

Centroptilum populations occurred in both Bigoray River and Stauffer 2. *Centroptilum* appeared to be a univoltine summer species. Populations appeared in early July, grew rapidly during the summer and emerged by mid-September (Fig. 13, 16).

Detritus was the major food component for both populations and accounted for essentially everything consumed except diatoms. All size classes of both populations averaged from 82 to 87% detrital ingestion. Diatom ingestion varied between 4 and 20% of total food consumed in Bigoray River and 12 and 20% at Stauffer 2 (Fig. 17). No seasonal or size class specific ingestion patterns were evident.

Animal remains and filamentous algae were not observed in any specimens. Mineral particles made up less than 1% of the total volume for all analyses, except in the Bigoray River population during July

1976, where sand accounted for about 3% of the total material consumed.

The total ingested food volume for all size classes except the 2-4 mm class was below the study average for both Centroptilum populations.

All size classes except Bigoray 8-10 mm nymphs ingested a greater than average quantity of small PSCI particles. The 4-6 and 6-8 mm classes had similar particle size distributions, while the 2-4 mm size class of the Bigoray River ingested a greater proportion of small particles than other size classes of the same population. Similar size individuals from Stauffer 2 consistently consumed more small particles than Bigoray specimens. There were no seasonal trends in total ingested volume or particle sizes at either site.

Other investigators report Centroptilum nymphs to consume primarily diatoms and often filamentous algae (Berner 1950, Ivanova 1958, Coffman 1967, Gilpin and Brusven 1970, Edmunds et.al. 1976). The range of diatom ingestion reported varied from 87% (Coffman 1967) to 30% (Edmunds et.al. 1976). Ivanova (1958) reported Centroptilum nymphs ingesting relatively large amounts of filamentous algae, up to 18% by volume.

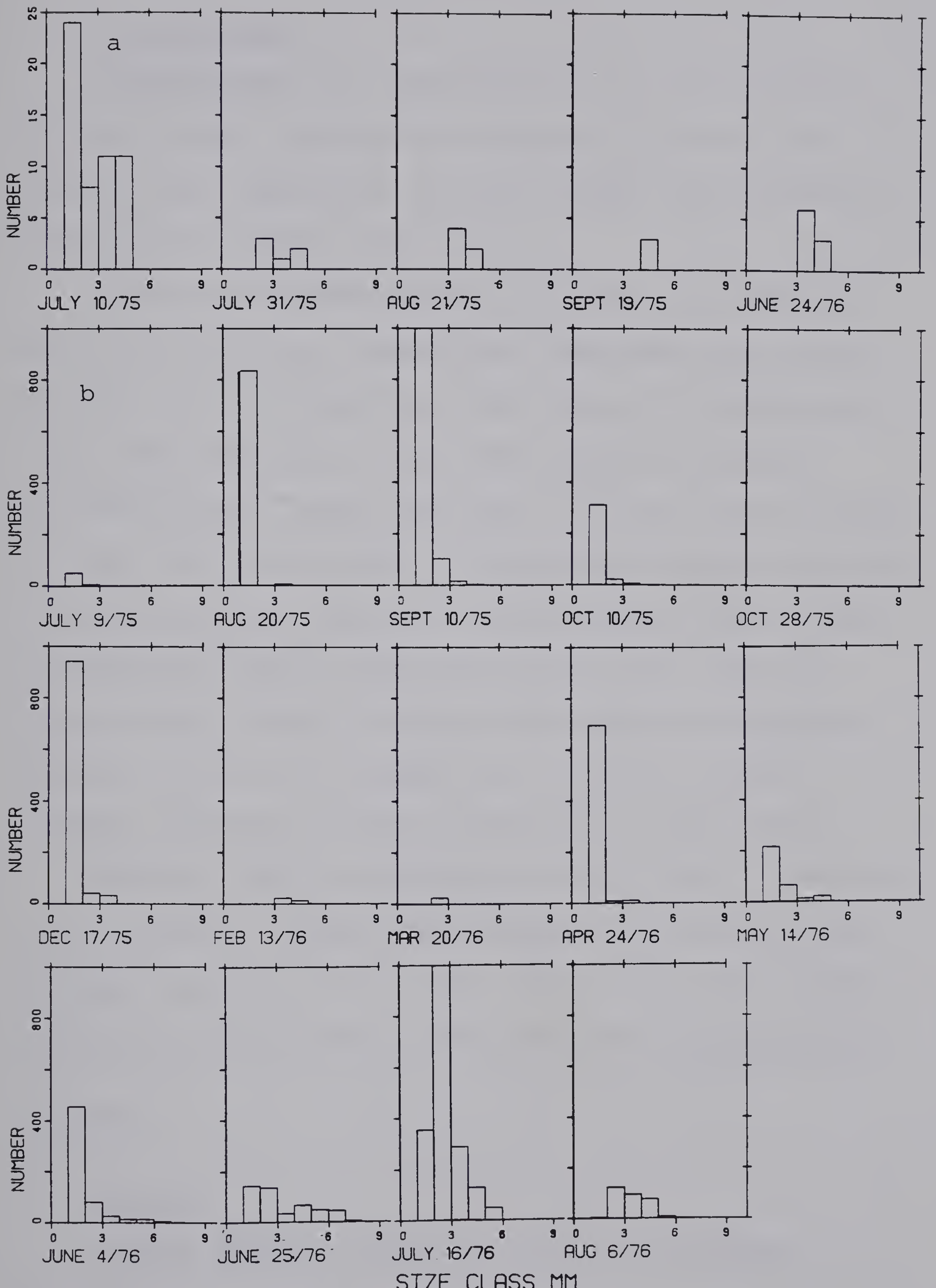

Figure 18. Number of Pseudocloeon sp. nymphs per mm size class, Tay River (a); Caenis simulans, Bigoray River (b).

Pseudocloeon

Pseudocloeon sp. occurred only in the Tay River. It was a summer species with hatching in June, very rapid growth especially in early summer, and emergence completed by October (Fig. 18).

Detritus composed 90-95% of material ingested in both June and July; insufficient specimens for stomach analysis were collected on other dates. No filamentous algae were observed in the three samples analyzed, and sand grains formed less than 1% of the total volume in July and 1.6% in June. I did not have enough specimens to detect seasonal and size class trends. Total volume of material ingested was below average for the two size classes studied, with no difference between June and July. The 2-4 mm nymphs had a slightly above average ingestion of small particles on both dates.

Coffman (1967) and Edmunds et.al. (1976), contrary to my findings, report *Pseudocloeon* to be herbivorous, whereas Shapas and Hilsenhoff (1976) found that diatom ingestion varied greatly among species of *Pseudocloeon*.

Caenidae

Caenis

Caenis simulans occurred only in the Bigoray River where it was a univoltine winter species (Fig. 18). The new generation first appeared in August with growth

extending into autumn. Possible delayed hatching continuing into spring occurred; there appeared to be little or no winter growth. Growth resumed in the spring, with emergence throughout the summer.

Caenis simulans was the only species that did not feed during winter. On 10 October 1975, almost all specimens had empty guts or only a small quantity of material in the hindgut. Throughout the winter, all the specimens analyzed had empty digestive tracts.

During the ice-free period, *Caenis* nymphs ingested usually greater than 95% detritus. This was slightly lower during summer 1976 (Fig. 17). There was a slight increase in diatom ingestion (relative to detritus) during summer 1976, and this coincided with Bigoray River's maximum epilithic diatom levels. There were no discernible differences between nymphal size classes in quantities of different food items ingested.

During spring and summer 1976, filamentous algae occurred consistently in the 2-4 mm size class nymphs but at levels always less than 0.2%. Filamentous algae were never found in the larger nymphs. Mineral particles were found consistently at the 0.5-1.0% level for all size classes.

The total food volume ingested was below the study average for all size classes. Seasonally, the summer individuals ingested a lower total volume than spring

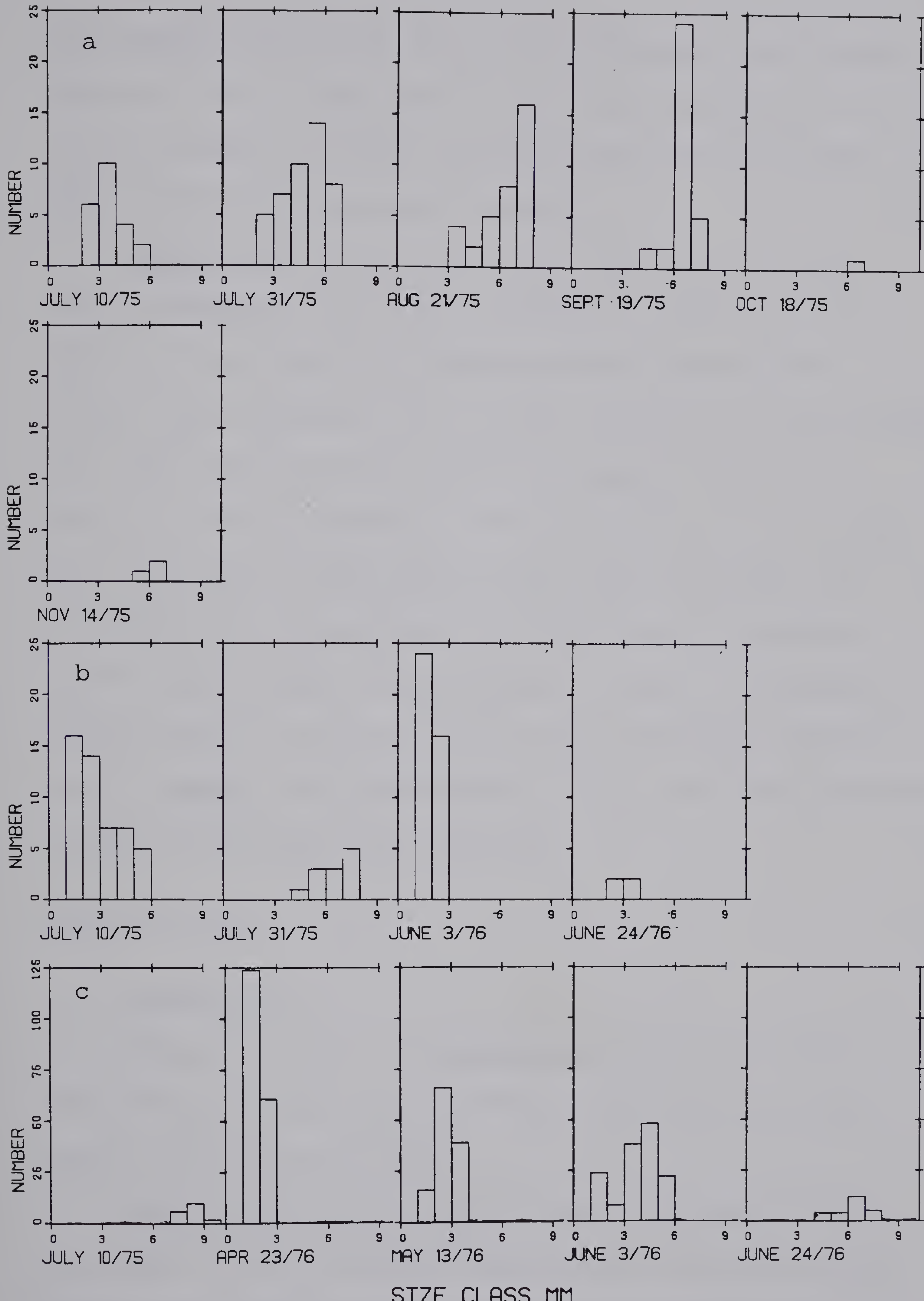

Figure 19. Number of <u>Ephemerella tibialis</u> nymphs per mm size class, Stauffer 1 (a); Tay River (b); and <u>E</u>. <u>flavilinea</u>, Tay River (c).

individuals. The size of particles ingested was above average, with a reduction in the PSCI compensated for by an increase in PSCII. Particle size distributions were similar in spring and summer.

Caenis inhabits mud and silt substrates (Berner 1950, Edmunds et.al. 1976); therefore predominantly detrital food habits is understandable (Moon 1938, Berner 1950, Edmunds et.al. 1976). Moon (1938) concluded that the lack of winter growth in *Caenis* nymphs was due to a lack of algae in the winter diet; he observed only detritus in the guts during winter and made no reference to a cessation of winter feeding. Coffman (1967) was the only investigator to report relatively large amounts of diatoms in the diet of *Caenis* nymphs. For *C. anceps*, he reported 97% of the total food ingested (based on calories) was detritus.

Ephemerellidae

Ephemerella

Numerous species of *Ephemerella* were collected from Stauffer Creek and Tay River, however none were found in the Bigoray River.

Ephemerella flavilinea was collected only in the Tay River. It is a summer species with an early spring hatch, very rapid spring growth, and an emergence that is complete by August (Fig. 19). The oviposited

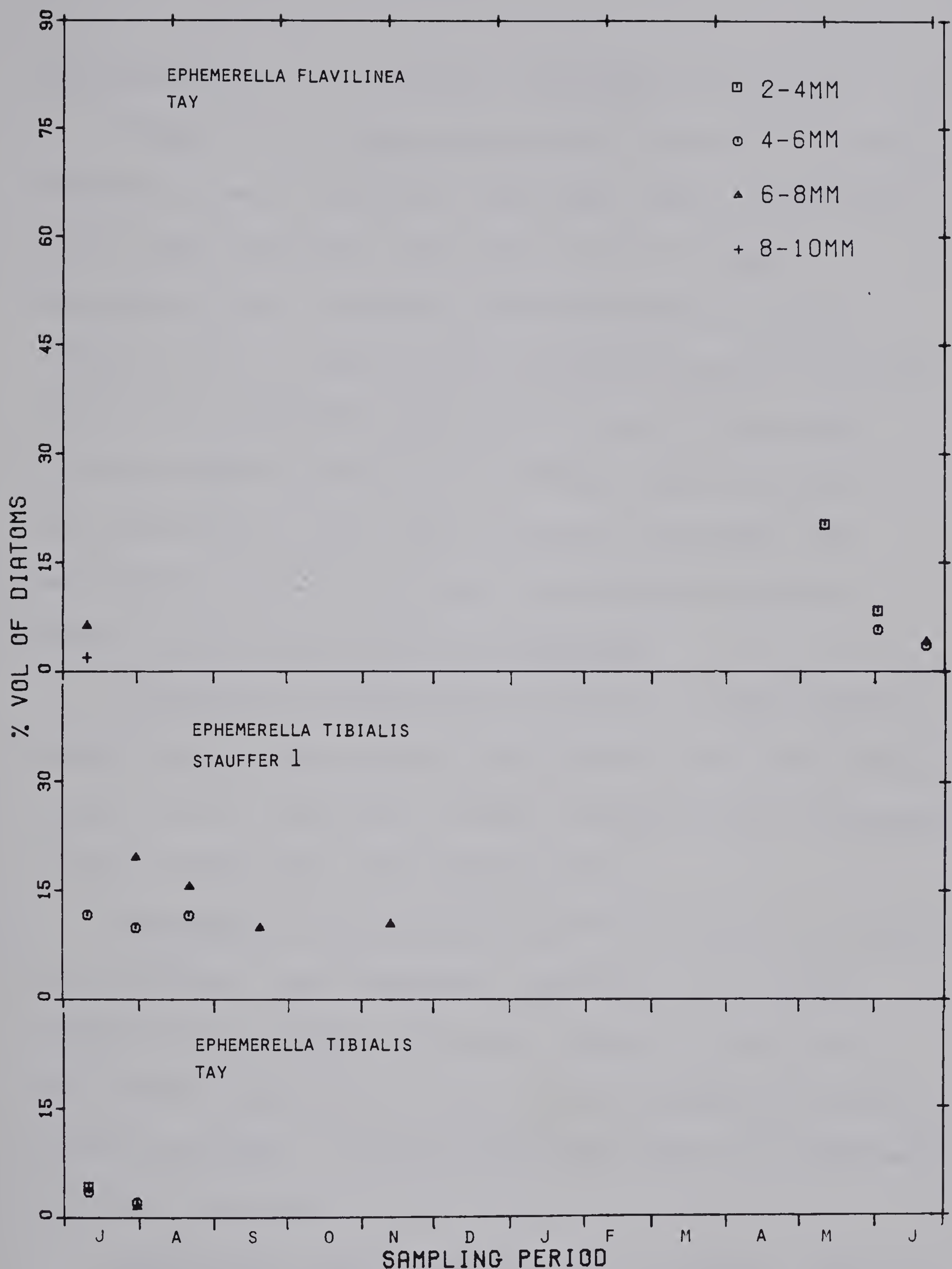

Figure 20. Proportion of ingested material composed of diatoms for the various size classes of *Ephemerella flavilinea* Tay River; *E. tibialis*, Stauffer 1 and Tay River (1975-1976).

eggs apparently lie dormant throughout the winter.

Nymphs of E. flavilinea greater than 4 mm usually consumed greater than 90% detritus. During early May 1976, when the first specimens of that summer's population were collected, 2-4 mm nymphs ingested close to 20% of their total consumed volume as diatoms (Fig. 20). Specimens analyzed during the remainder of that summer contained relatively fewer diatoms, less than 10% of the total material consumed. The peak diatom ingestion in May correlated with Tay River's spring epilithic diatom peak.

Filamentous algae occurred only in trace amounts. Mineral particles composed less than 1.0% of the total volume for all analyses. Animal fragments were recorded in one 6-8 mm gut sample during July.

Ephemerella flavilinea specimens ingested slightly below average total volumes, especially the larger nymphal size classes. The only seasonal trend was a late spring increase in total food consumption by the 2-4 mm specimens. This is coincident with an increased detrital ingestion.

Ephemerella flavilinea had above average ingestion of small particles (72% PSCI) by 2-4 mm nymphs and below average for other size specimens (50-60% PSCI). There was an increase in the size of particles ingested from May to June 1976.

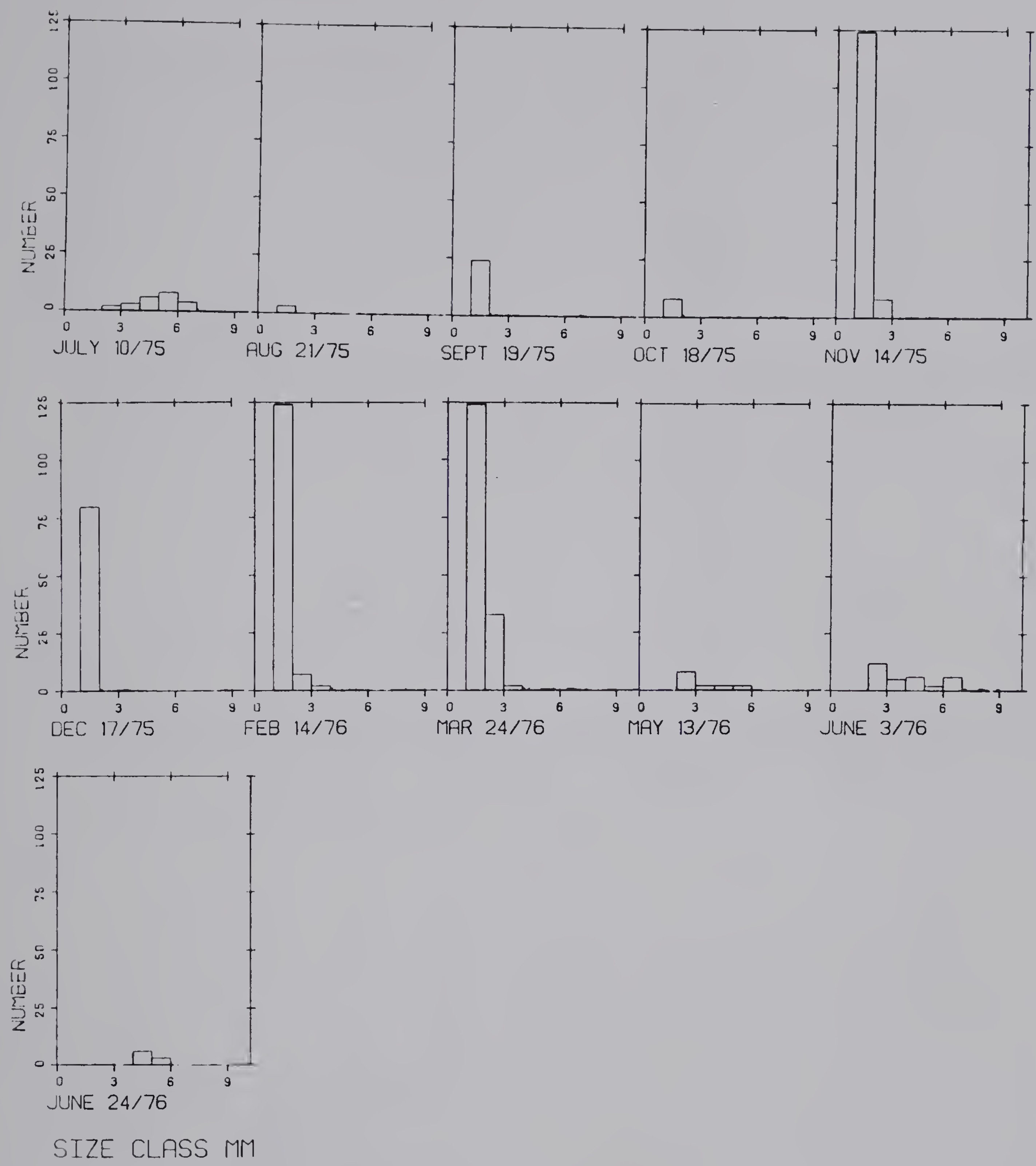

Figure 21. Number of Ephemerella inermis nymphs per mm size class, Tay River.

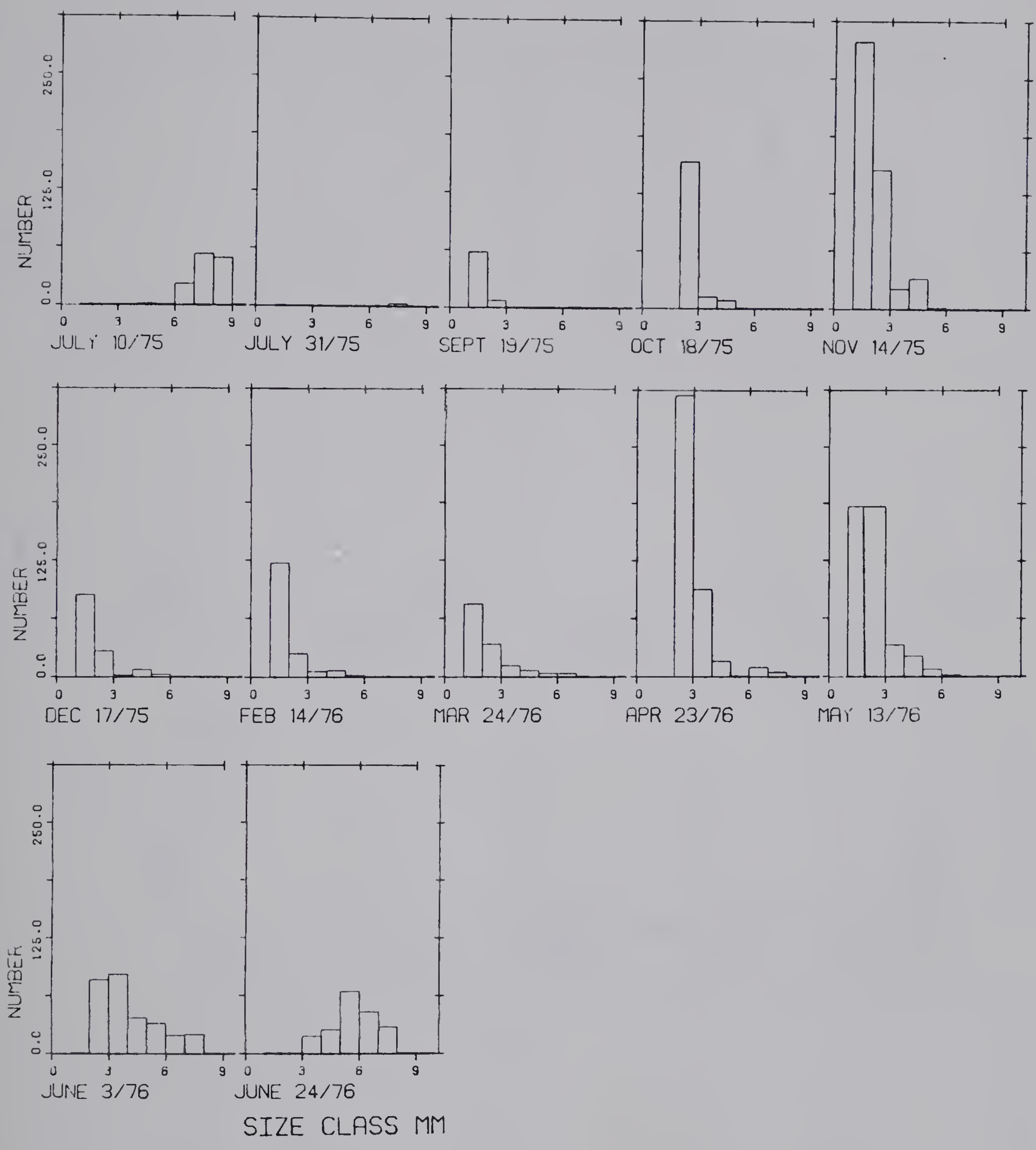

Figure 22. Number of Ephemerella inermis nymphs per mm size class, Stauffer 2.

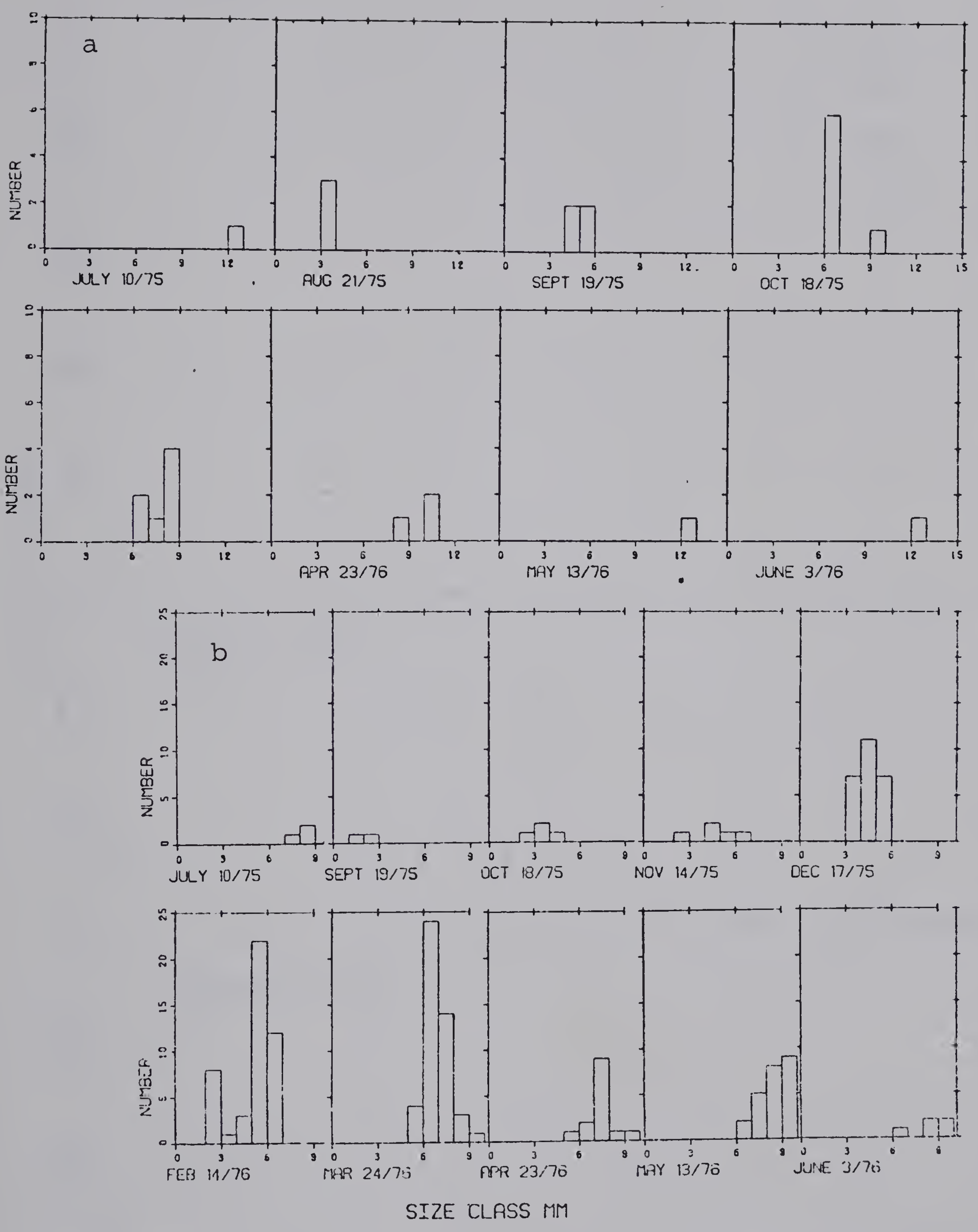

Figure 23. Number of Ephemerella spinifera nymphs per mm size class, Tay River (a); E. inermis Stauffer 1 (b).

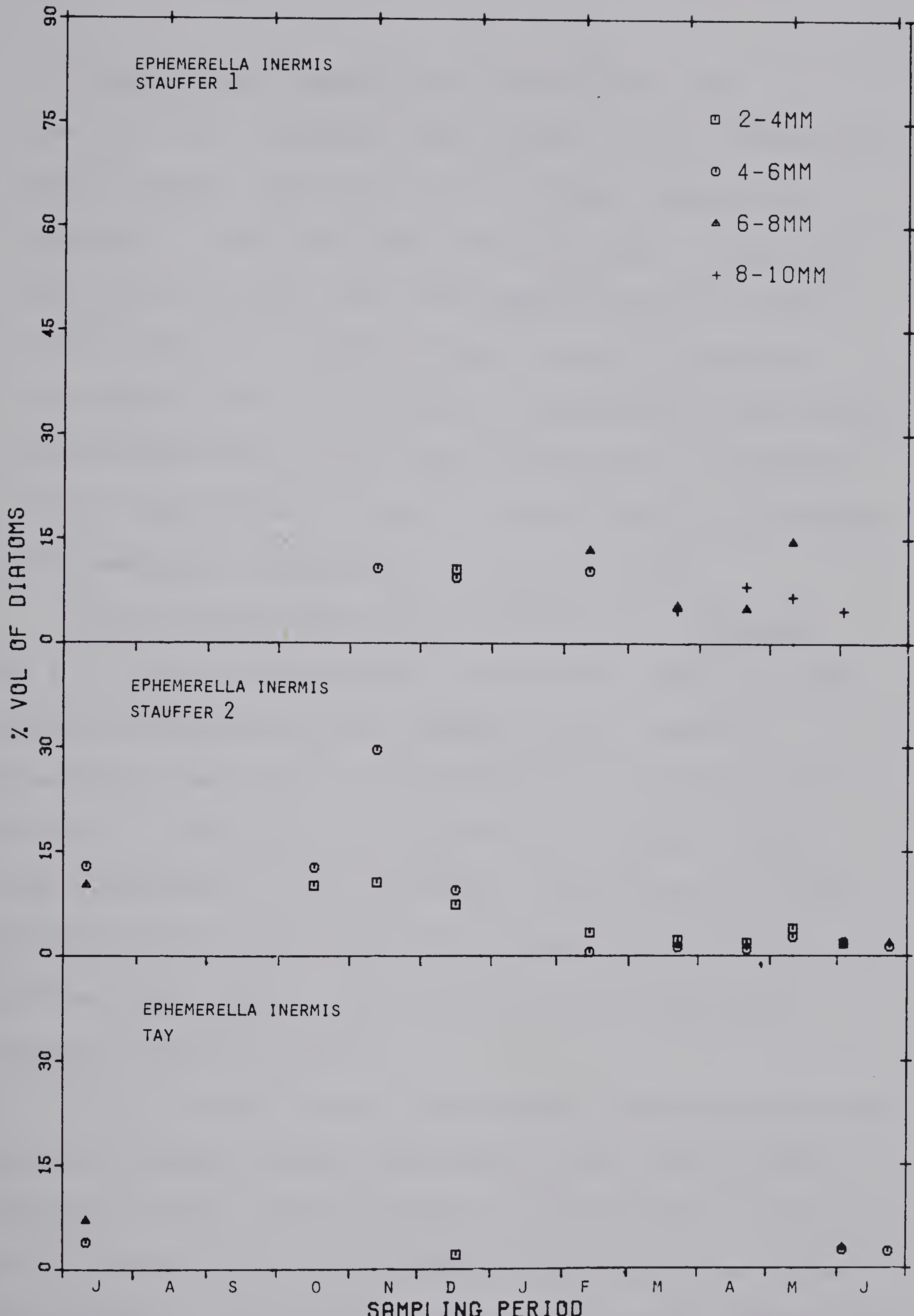

Figure 24. Proportion of ingested material composed of diatoms for the various size classes of Ephemerella inermis nymphs Stauffer 1, Stauffer 2 and Tay River (1975-1976).

Ephemerella inermis was found in the Tay River and both Stauffer Creek sites. It is a univoltine winter species. The 2-4 mm class first appeared in September at Stauffer Creek and in August in the Tay River (Fig. 21, 22, 23). The nymphs exhibited rapid autumn growth in Stauffer Creek; however this was less apparent for the Tay River population. Slow winter growth occurred, but was less pronounced at Stauffer 1 than at other sites. A spring growth period was evident with emergence complete by the end of July.

The dominant food item ingested by *E. inermis* at all sites was detritus. The average proportion of detritus ingested by all nymphal size classes at Stauffer 1 was close to 90%, between 92% and 96% at Stauffer 2, and greater than 95% for all but 6-8 mm size specimens in the Tay River. Large nymphs at both Stauffer Creek sites usually ingested more detritus than smaller size nymphs, whereas in the Tay River the reverse trend occurred.

At all three sites, the highest diatom consumption occurred during summer and autumn (Fig. 24). At both Stauffer sites, diatoms made up approximately 10-15% of the total ingested material, with the 4-6 mm class at Stauffer 2 achieving a high of 30% diatom consumption. A decline in diatoms consumed, coinciding with a reduction in epilithic diatoms, occurred in December at Stauffer 2,

but not until late February at Stauffer 1. Late winter and spring diatom consumption levels were lowest in Tay River and Stauffer 2 compared to Stauffer 1. At the Stauffer Creek sites there was a slight May increase in diatom ingestion, coincident with a small epilithic diatom peak.

Filamentous algae were found in *E. inermis* nymphs occasionally during late autumn and winter in trace quantities. These algae were never detected in the Tay River population. Mineral particles, although consistently present, never made up more than 2.5% of total material consumed at any site. During July, a few animal fragments were found in larger specimens.

Total food volume consumed by *E. inermis* nymphs was above the study average for all Stauffer 1 size classes and the 6-8 mm nymphs at Stauffer 2. Total food volume consumed was below average for other Stauffer 2 nymphs and all Tay River specimens. Seasonally, the greatest amount of food consumed was during spring at all sites.

The size of particles consumed by *E. inermis* at all sites was slightly above average except for 2-4 mm nymphs at Stauffer 2 and Tay River. At all sites there was a steady decline in consumption of less than 32 um diameter particles as the nymph increased in size. Highest consumption of small particles occurred in autumn, with the highest proportion of large particles

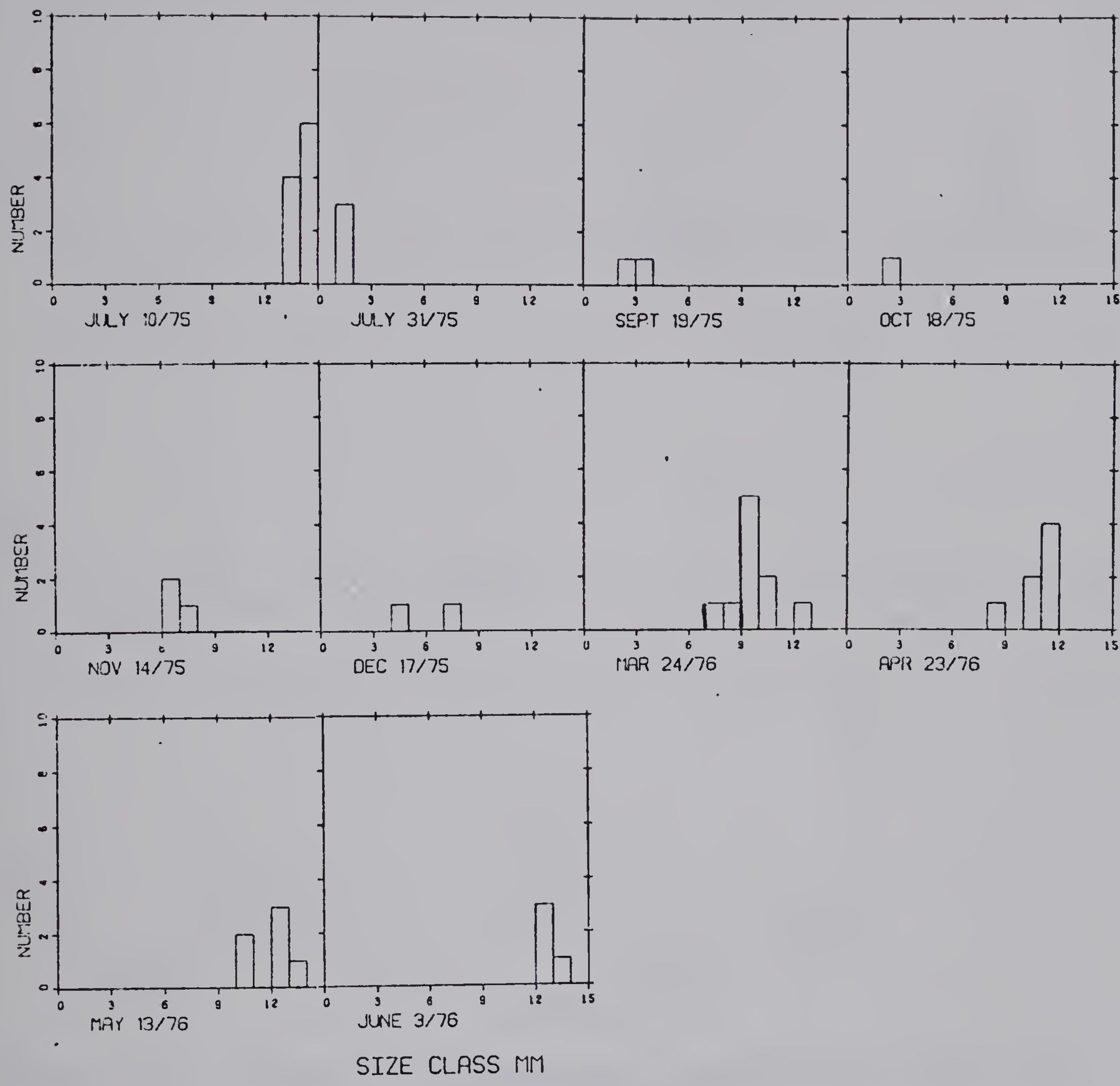

Figure 25. Number of Ephemerella spinifera nymphs per mm size class, Stauffer 1.

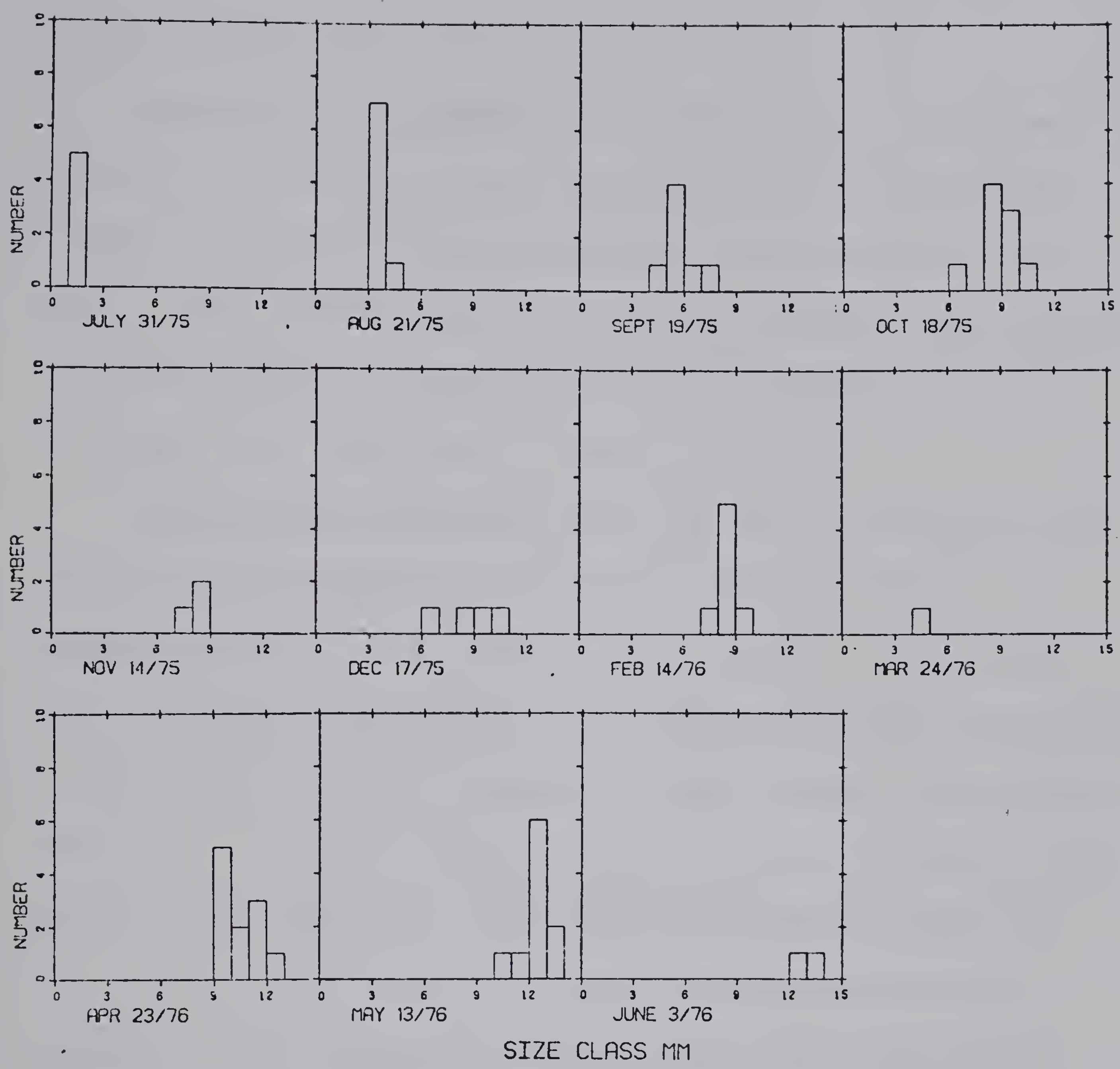

Figure 26. Number of Ephemerella spinifera nymphs per mm size class, Stauffer 2.

being consumed in spring.

Ephemerella spinifera occurred in the Tay River and at the Stauffer Creek sites. It is a univoltine winter species with eggs hatching in late July (Fig. 23, 25, 26). There was rapid autumn growth, some growth in winter, and a resumption of rapid growth in spring. Emergence was completed in July.

Ephemerella spinifera was the only ephemeropteran studied that ingested relatively large quantities of animal material. The larger size classes, 6-8 mm and up, contained substantial quantities of animal material. It was not possible to quantify (by volume) the amount ingested. Scans of the membrane filters indicated that insect head capsules, legs, and mouthparts were the dominant gut contents. The only recognizable animal fragments were ephemeropteran nymphs and chironomid larvae. The large amount of animal material ingested would indicate *E. spinifera* nymphs are at least facultative predators, rather than incidental consumers of dead animal material. Even if predaceous, it likely obtained considerable nutrition from the significant quantities of detritus and diatoms consumed.

Detritus, including animal tissue, accounted for greater than 95% of all material ingested by *E. spinifera* at Stauffer 1. Nymphs obtained from Stauffer 2 exhibited increased detrital ingestion as

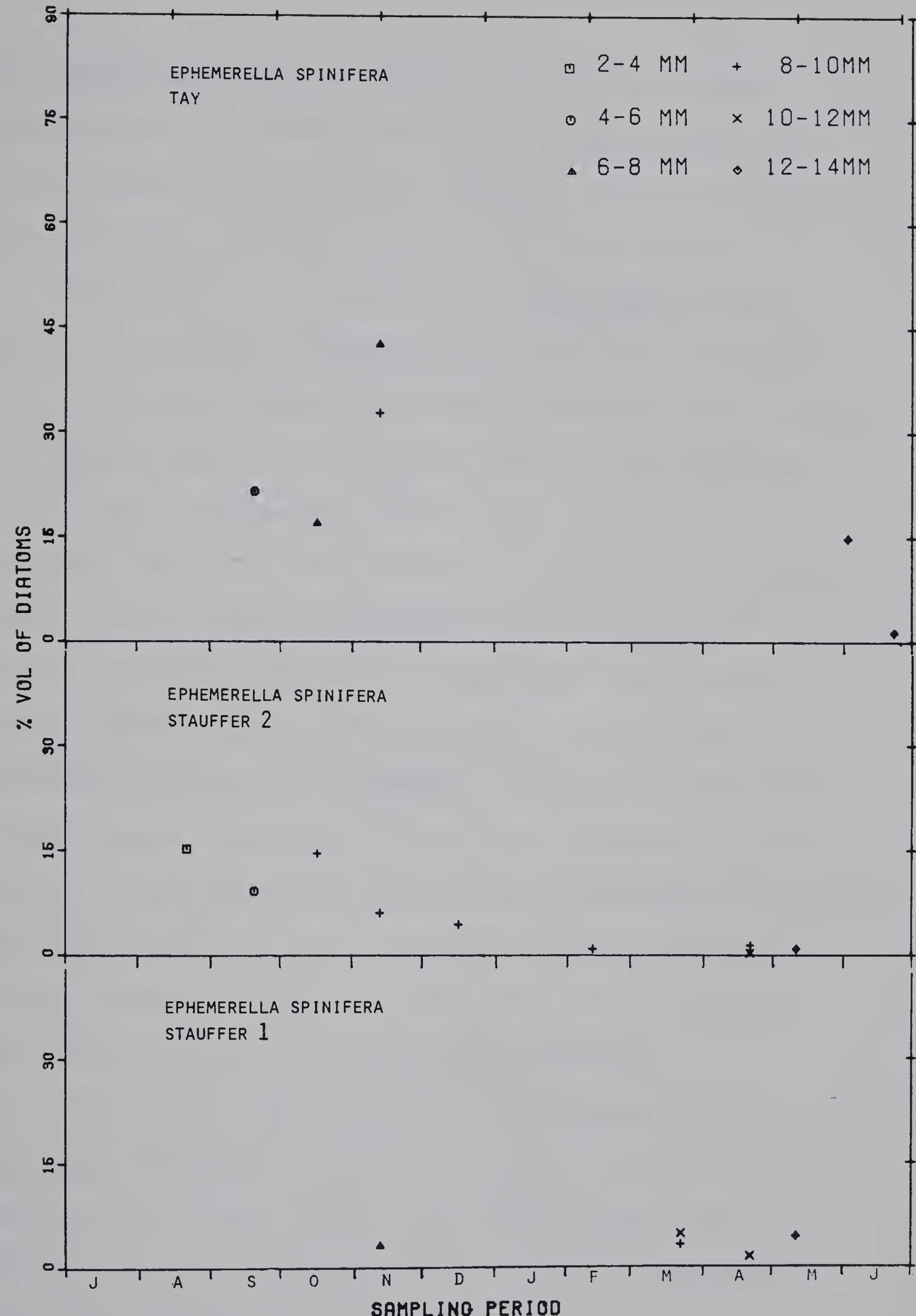

Figure 27. Proportion of ingested material composed of diatoms for the various size classes of Ephemerella spinifera nymphs, Tay River, Stauffer 2 and Stauffer 1 (1975-1976).

the nymphs increased in size, e.g. 85% for 2-4 mm specimens and up to 99% for 12-14 mm specimens. Tay River specimens had variable rates of detrital ingestion, with averages as low as 67% for 8-10 mm nymphs.

Consumption of diatoms by _E_. _spinifera_ nymphs varied considerably between sites, seasons, and size classes. The Tay River population ingested more diatoms than populations at the other sites, varying between 15 and 25% in September and October and 45% in November (Fig. 27). No specimens were analyzed during winter. April and June analyses indicated reduced diatom ingestion. Stauffer 2 specimens had a peak summer diatom consumption of 10-15%, which then decreased, starting in November, to very low levels during winter and spring. The diatom ingestion of the Tay River and Stauffer 2 populations increased coincident with the increase in the epilithic diatom populations. During winter and spring, there was almost complete dependence on detritus and animal material.

Filamentous algae were never detected in _E_. _spinifera_ stomachs. Mineral particles at all sites averaged less than 0.5% of the total volume, the exception being 2.6% sand from an 8-10 mm Stauffer 2 specimen in December.

The total food volume ingested by _E_. _spinifera_ tended to be above average for size classes under 8 mm,

and below average for larger size nymphs. The change in relative consumption coincides with the size at which animal ingestion becomes more important.

The size distribution of particles ingested is close to the study average for specimens up to 8 mm; all larger size classes had an increase in consumption of large particles in PSC ranges II and III (64-161 um). This again correlates with the switch to greater ingestion of large particles during winter and spring.

Ephemerella tibialis is found in Tay River and Stauffer 1. It had a univoltine summer life cycle, the nymphs being collected from the Tay River only in June and July (Fig. 19). At Stauffer 1, nymphs were found from July until September, with a few specimens collected as late as November. The differences in life cycles between the two sites may be a function of Stauffer 1's relatively cooler summer and warmer autumn water temperatures.

Both *E. tibialis* populations ingested mostly detritus. The two size classes of nymphs analyzed from Stauffer 1 averaged 85 to 88% detritus ingestion. All size classes of nymphs from the Tay River averaged greater than 95% detrital material in the guts.

The differing rates of detrital consumption between populations was reflected in a greater diatom consumption by the Stauffer 1 nymphs (Fig. 20). Stauffer 1 individuals consumed between 10 and 20% diatoms by volume,

with peak consumption being in late July and August. Tay River specimens consumed less than 5% diatoms on both dates in July, the only period for which I had a sufficient number of specimens for analysis. Size class differences were evident only amongst Stauffer 1 nymphs; 6-8 mm class ingested more diatoms than 4-6 mm specimens throughout the summer. The low diatom consumption in Tay River coincided with relatively low epilithic diatom populations in July; however at Stauffer 1, the September-October epilithic peak is not reflected in the composition of the food consumed.

Neither animal fragments nor filamentous algae were evident in any stomachs analyzed. Mineral particle consumption by the Tay River and Stauffer Creek populations was always less than 2.0%.

Total volume of material ingested by *E. tibialis* nymphs was considerably higher than the study average for all size classes from both sites. No seasonal trends were discernible, except that autumn specimens from Stauffer 1 ingested less material than summer individuals of the same size.

Size of ingested particles was near the study average for Tay River specimens less than 6 mm. All 6-8 mm specimens from both populations, along with 4-6 mm Stauffer 1 individuals, consumed a greater than average proportion of large particles, particularly

in the 32-64 um diameter range (PSCII). Seasonally, Stauffer 1 individuals ingested a greater proportion of small particles in the autumn than during summer.

Trophic habits of Ephemerella species have been frequently studied and found to be diverse. Ephemerella ignita, a Palaearctic species that has been studied most often, lives mainly in crevices and interstices where it ingests mostly detritus (Ivanova 1958, Calow 1974b; however Gaevskaya (1966) reported mostly macrophytes in the guts of E. ignita. Moore (1977) reported detritus as the main diet of two Nearctic Ephemerella species from the arctic. Diatoms, desmids and filamentous algae have been reported as dominant food materials for other Ephemerella species (Percival and Whitehead 1929, Jones 1950, Minckley 1963). Researchers who have sampled through several seasons or investigated more than one species have reported Ephemerella to exploit a wide range of food material, depending on the species and time of sampling (Muttkowski and Smith 1929, Coffman 1967, Shapas and Hilsenhoff 1976).

Ephemeridae

Ephemera

Ephemera simulans was the only member of the genus studied and occurred at Stauffer 2 and Bigoray River. It appears to have at least a two

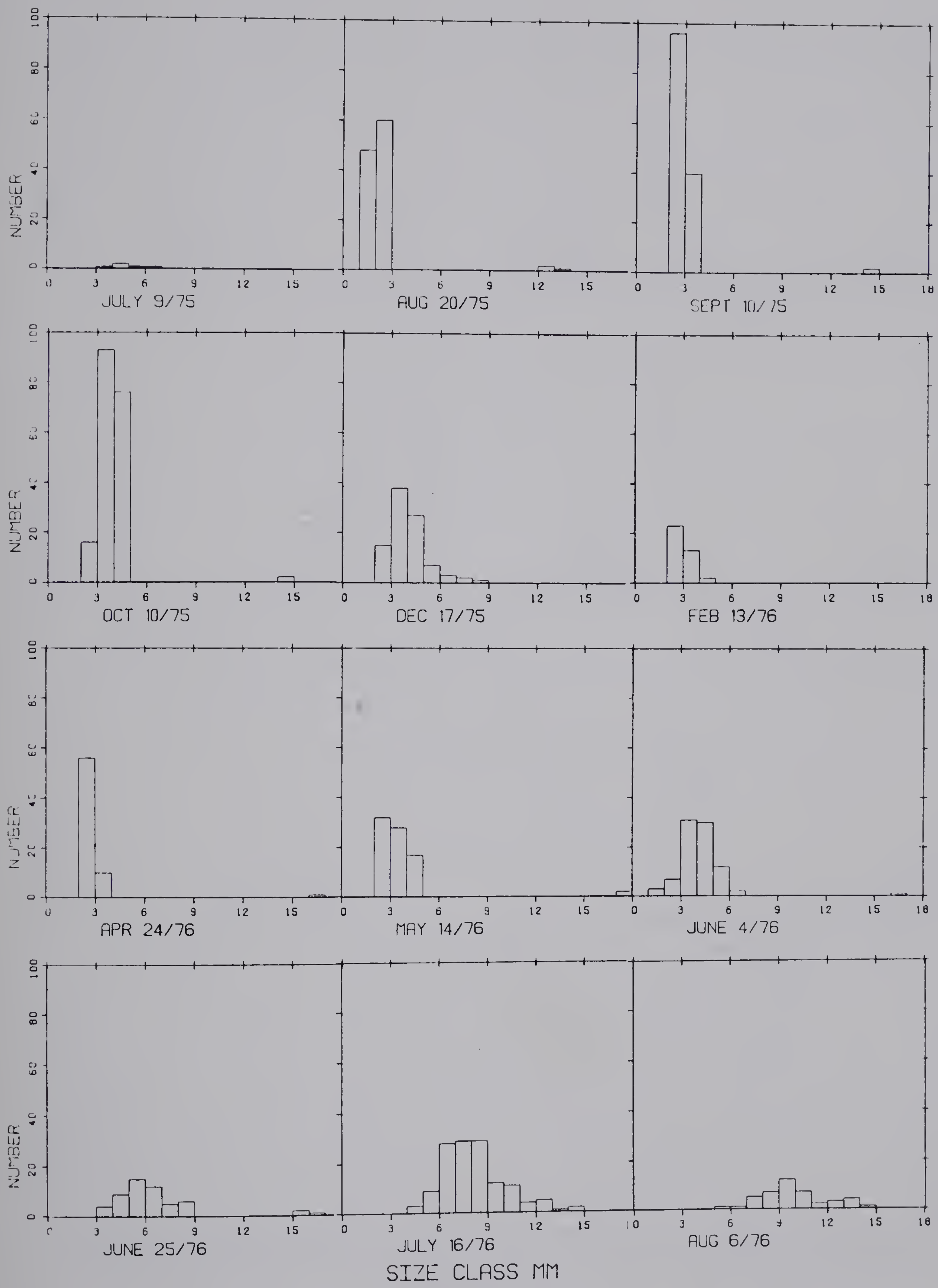

Figure 28. Number of Ephemera simulans nymphs per mm size class, Bigoray River.

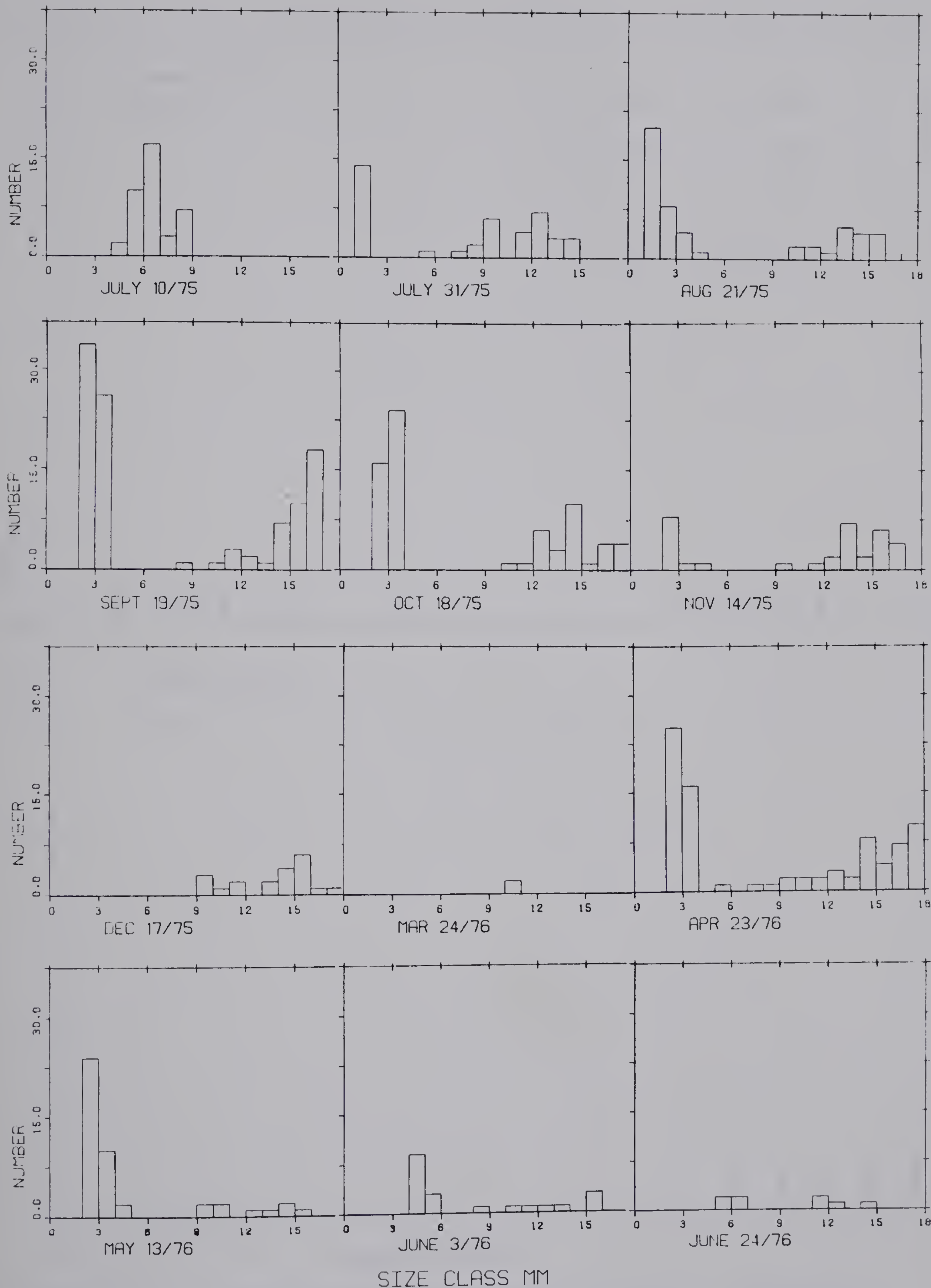

Figure 29. Number of Ephemera simulans nymphs per mm size class, Stauffer 2.

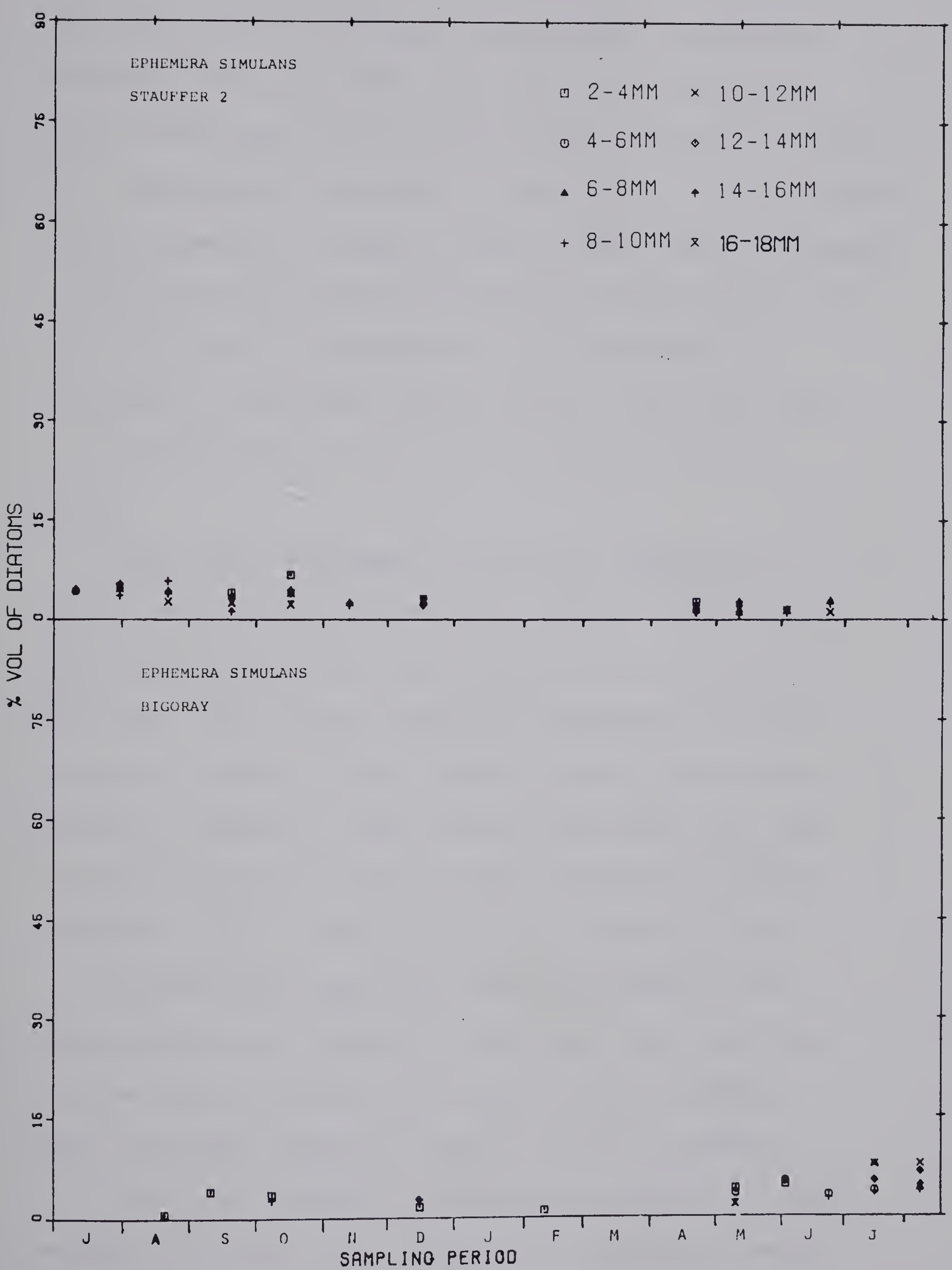

Figure 30. Proportion of ingested material composed of diatoms for the various size classes of <u>Ephemera simulans</u> nymphs, Stauffer 2 and Bigoray River (1975-1976).

year life cycle, with very large nymphs collected throughout the year (Fig. 28, 29). The young of a cohort were first collected in late summer and autumn, with some growth occurring at that time. During winter, growth appeared to cease at both sites. Growth resumes in the spring and extends throughout the summer. From the life history histograms it is impossible to determine if emergence starts during the first year or is restricted to the second year of the life cycle.

Food habit analyses indicate E. simulans is almost entirely dependent on detritus, since diatoms usually comprised less than 5% of the food in the gut (Fig. 30). Slight sporadic increases in diatom consumption were evident during summer and autumn months at Stauffer 2 and during mid-summer for the Bigoray River populations. These increases roughly coincide with increased epilithic standing crops.

Filamentous algae and animal fragments were undetected in all samples. Sand particles remained at less than 1% except for Bigoray River nymphs, which attained levels as high as 2.5% in summer.

The total volume of particles consumed is below average for most size classes, the exception being some large specimens that approximate or occasionally exceed the mean study average for their size class.

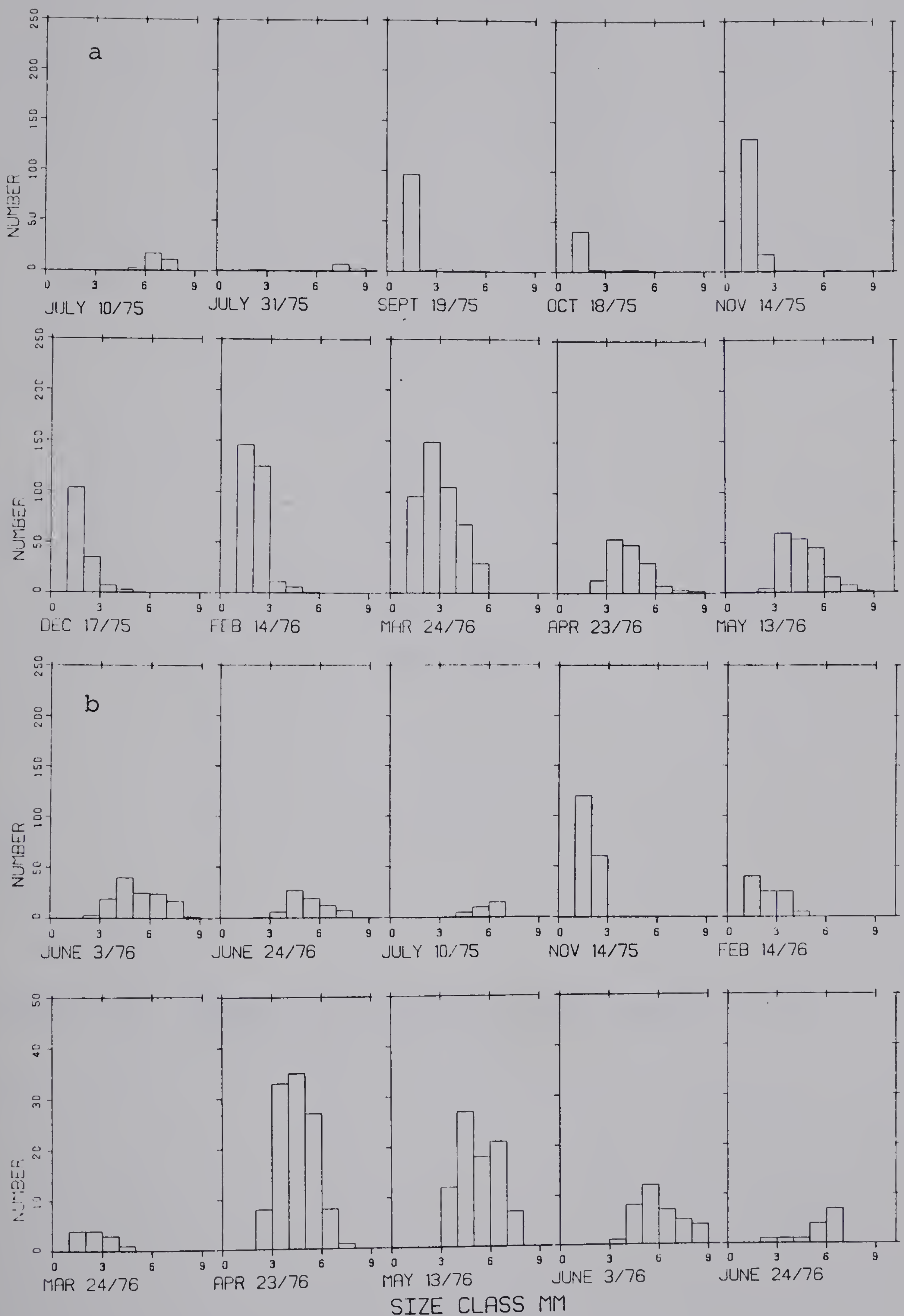

Figure 31. Number of <u>Cinygmula mimus</u> nymphs per mm size class, Stauffer 1 (a); Stauffer 2 (b)

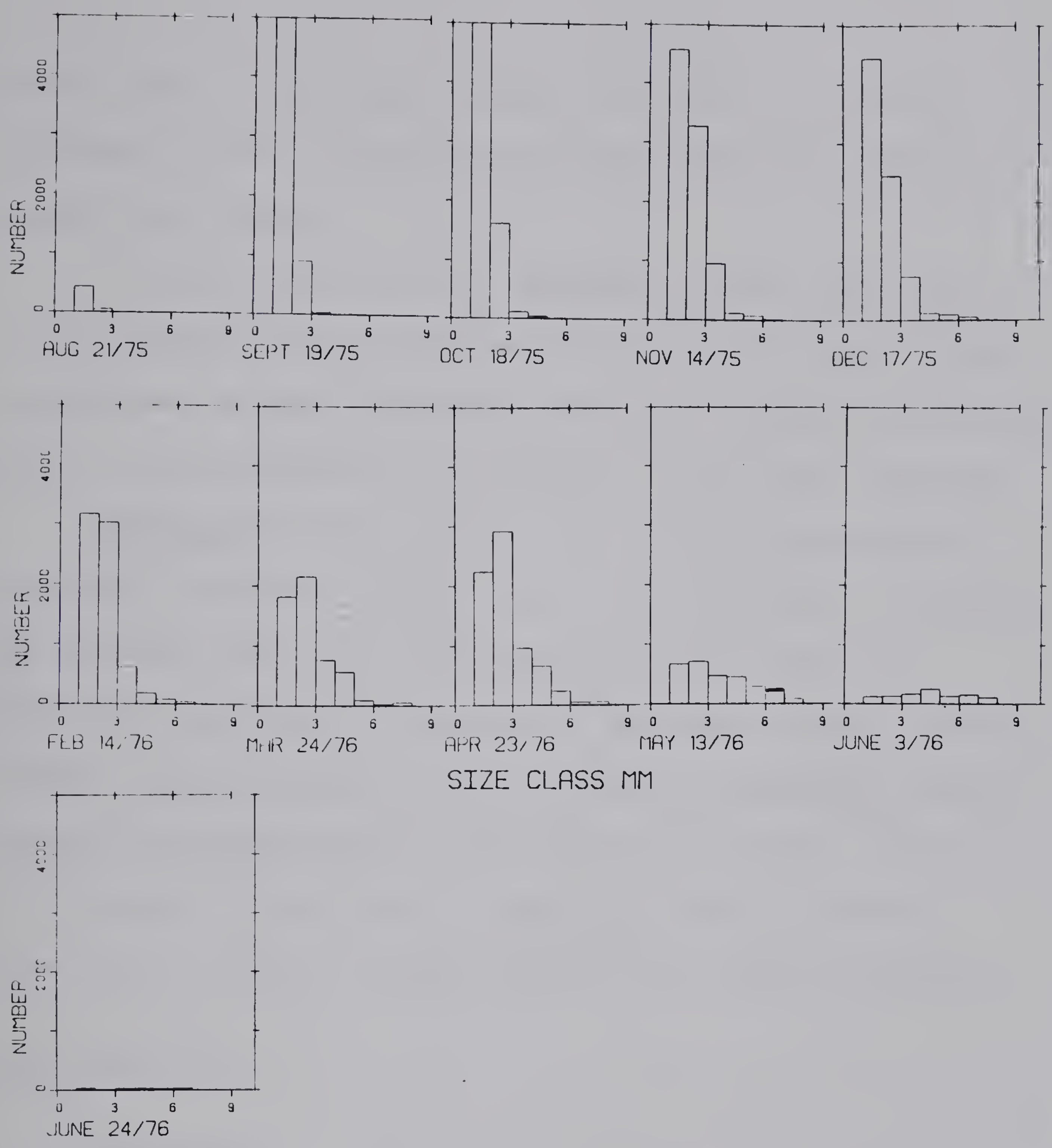

Figure 32. Number of Cinygmula mimus nymphs per mm size class, Tay River.

There were no seasonal trends in total food volume consumed, being relatively uniform throughout spring, summer and autumn.

At both locations, E. simulans nymphs less than 6 mm ingested above average proportions of small PSCI particles. Larger specimens generally consumed particles with a size distribution similar to the study average.

Ephemera's food habits have not been extensively studied. Wissmeyer (1926) reported ingestion of between 50 and 86% detritus, the remainder being diatoms, sphagnum, macrophyte fragments, and some animal material. Shapas and Hilsenhoff (1976) report E. simulans nymphs ingesting approximately 95% detritus. Coffman (1967), in contrast, concluded E. simulans nymphs received over 85% of their caloric intake from animal material.

Heptageniidae

Cinygmula

Cinygmula mimus, a Cordilleran species, was abundant at all sites except the Bigoray River. Its life history is that of a univoltine winter species; small nymphs first appeared in late summer at Stauffer 1 and Tay River, but not until November at Stauffer 2 (Fig. 31, 32). There was rapid autumn and spring growth and slower growth during winter. Emergence occurred during late spring and summer.

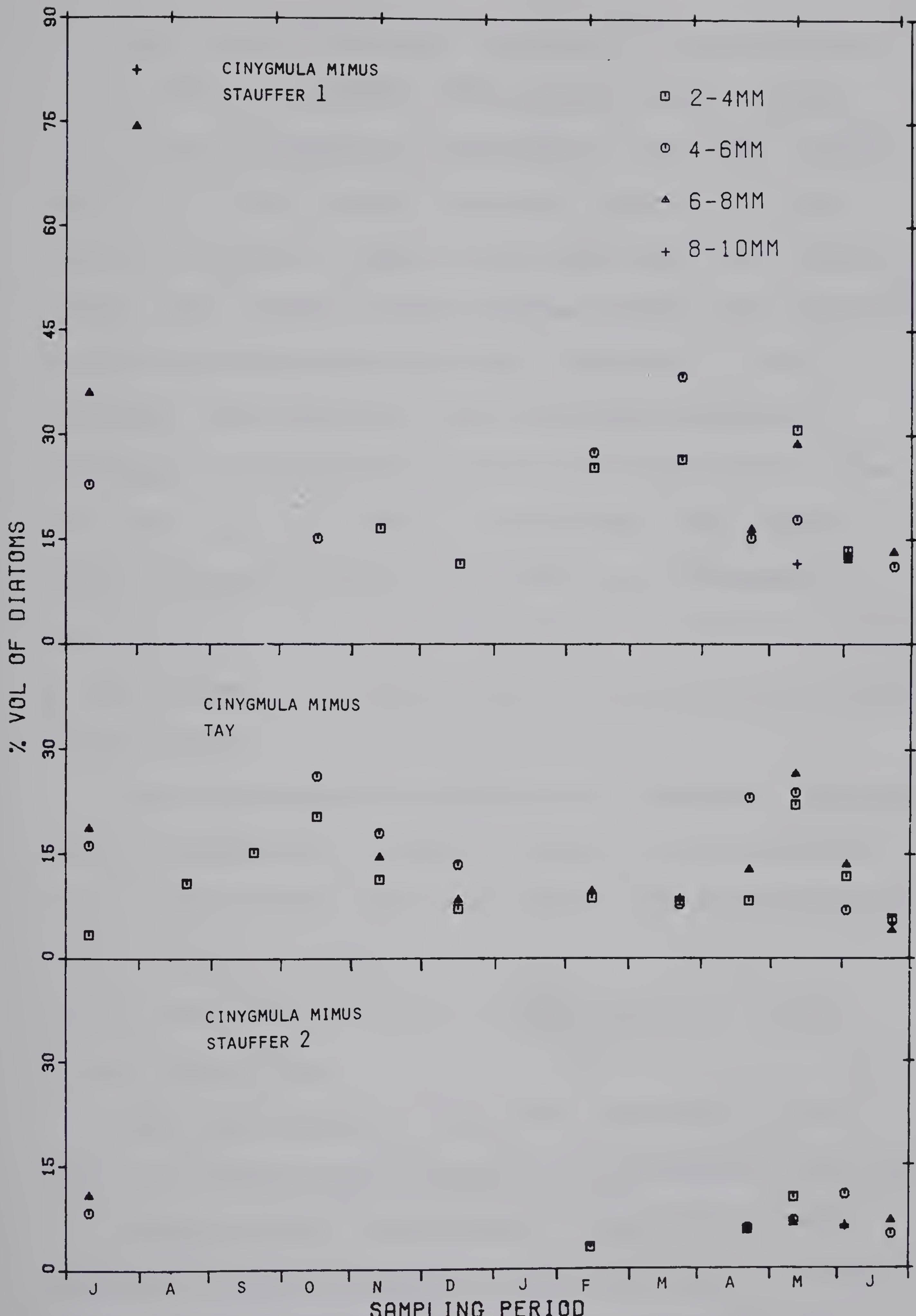

Figure 33. Proportion of ingested material composed of diatoms for the various size classes of Cinygmula mimus Stauffer 1, Tay River and Stauffer 2 (1975-1976).

The ratio of diatoms to detritus ingestion was variable both seasonally and between sites. During July, diatom ingestion at Stauffer 1 was high, particularly on 31 July, when the large nymphs (6-10 mm) ingested between 75 and 85% diatoms (Fig. 33). During autumn, the 2-4 and 4-6 mm classes of the new generation ingested predominantly detritus (85-90% of volume consumed). During late winter, diatom consumption increased to between 25 and 35%, falling again to the 15% level in spring (AMJ). Significant size class trends included high July consumption of diatoms by nearly mature nymphs and an increasing diatom consumption by small nymphs starting in early autumn and continuing through March.

The high diatom consumption by Stauffer 1 Cinygmula was not evident at Stauffer 2. Detritus accounted for 90% or more of the total material in all guts analyzed. Lowest diatom consumption occurred in February, with a slight increase by 2-4 and 4-6 mm specimens during May and early June.

Epilithic standing crops from Stauffer 1 and 2 did not correlate well with diatom consumption patterns of C. mimus nymphs. At Stauffer 1, high July diatom ingestion occurred before the epilithic peak, and the February-March consumption peak coincided with an epilithic decline. Stauffer 2 epilithic standing crops

were very high in July; however, this was not reflected in the stomach samples. The slight May-June increase in diatoms consumed at Stauffer 2 was coincident with a diatom standing crop increase.

Detrital ingestion by Tay River _C. mimus_ was intermediate between the _C. mimus_ populations of Stauffer 1 and Stauffer 2. Average detrital ingestion amongst size classes fluctuated from 83 to 88%. Diatom consumption varied from highs of near 30% during October and May to lows near 5% during early July and late winter. Relative diatom ingestion by the Tay River population closely followed the spring and autumn epilithic diatom standing crop peaks.

Cinygmula nymphs never had animal material or filamentous algae in their guts. Mineral particle consumption was usually below 1%.

Total volume of material ingested was slightly below the study average for all Stauffer 1 size classes. Peak consumption occurred in spring, except for the 6-8 mm class which had highest ingestion during summer. With the exception of 6-8 mm specimens, the Stauffer 2 population consumed slightly greater than average volumes of material. The only significant size class trend was the reduced total food volume in summer. For the Tay River populations, total volumes consumed were above the study average for 2-4 mm nymphs and below

average for larger nymphs. Seasonally, 2-4 mm nymphs ingested more material in summer than at other times. During autumn, 4-6 mm specimens had their peak ingestion of material, whereas 6-8 mm nymphs consumed more in winter than at any other times.

Size of particles ingested were generally smaller than average for all size classes from all sites. At both Stauffer Creek sites, 2-4 mm nymphs consumed relatively more small particles than did the other size class nymphs. The Stauffer 1 population ingested a greater proportion of large particles (PSCII & III) during spring; however, throughout the rest of the year the nymphs consumed above average proportions of PSCI particles. Stauffer 2 nymphs had a slightly depressed consumption of small particles during summer. The Tay River population consumed greater proportions of larger particles during summer; small particles were most important in spring.

Variable seasonal patterns in consumption of detritus and diatoms by _C. mimus_ populations have been noted by Chapman and Demory (1963), who report diatom consumption varying between 4 and 80%, with the highest value occurring in spring. Gilpin and Brusven (1970) give a mean diatom consumption of 35% for _C. mimus_ nymphs. Moore (1977), for an arctic population of _C. tarda_, observed diatom volumes of 25-35% during the summer, followed by a reduction to 6-8% in winter.

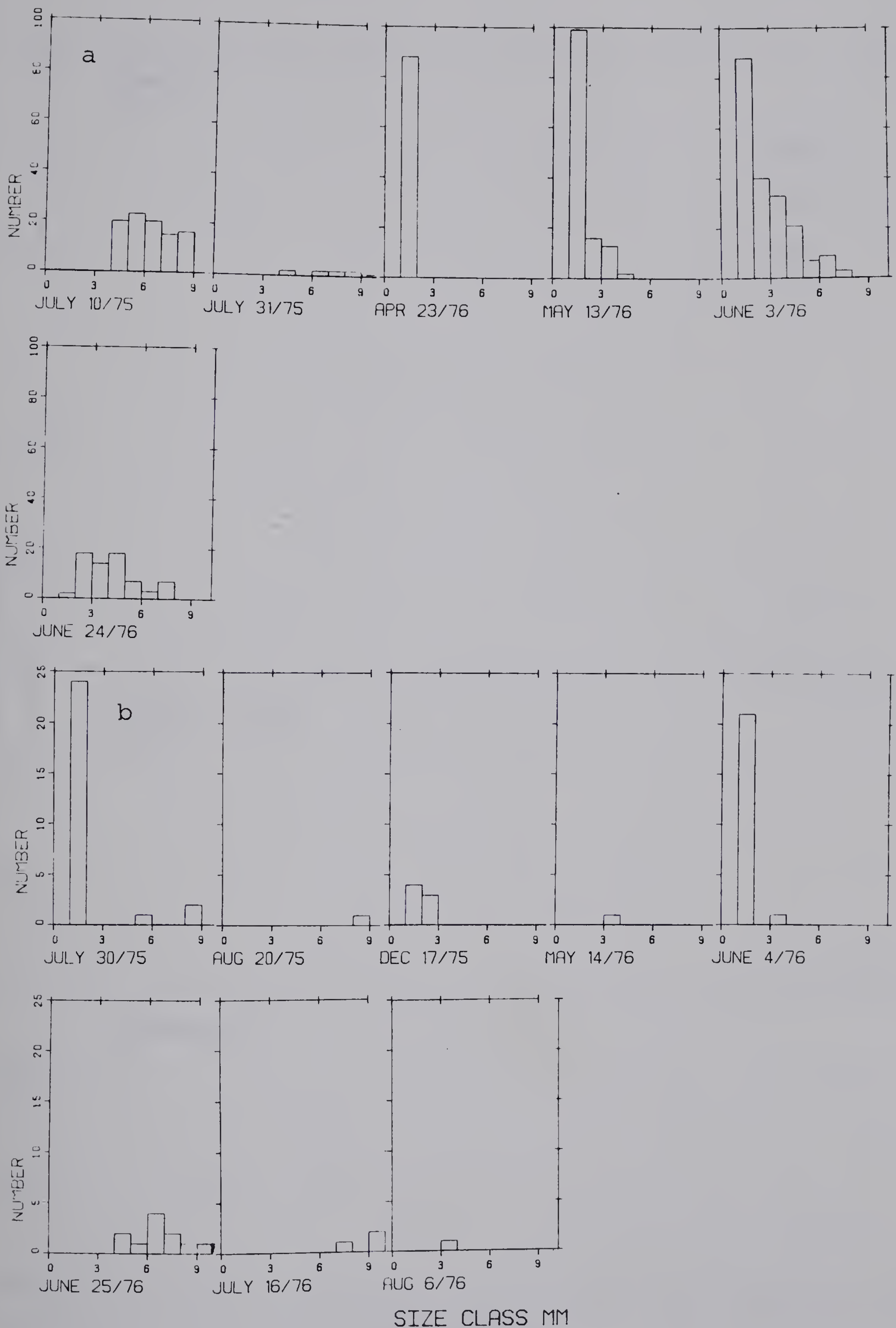

Figure 34. Number of _Epeorus_ sp. nymphs per mm size class, Tay River (a); _Stenacron canadense_, Bigoray River (b).

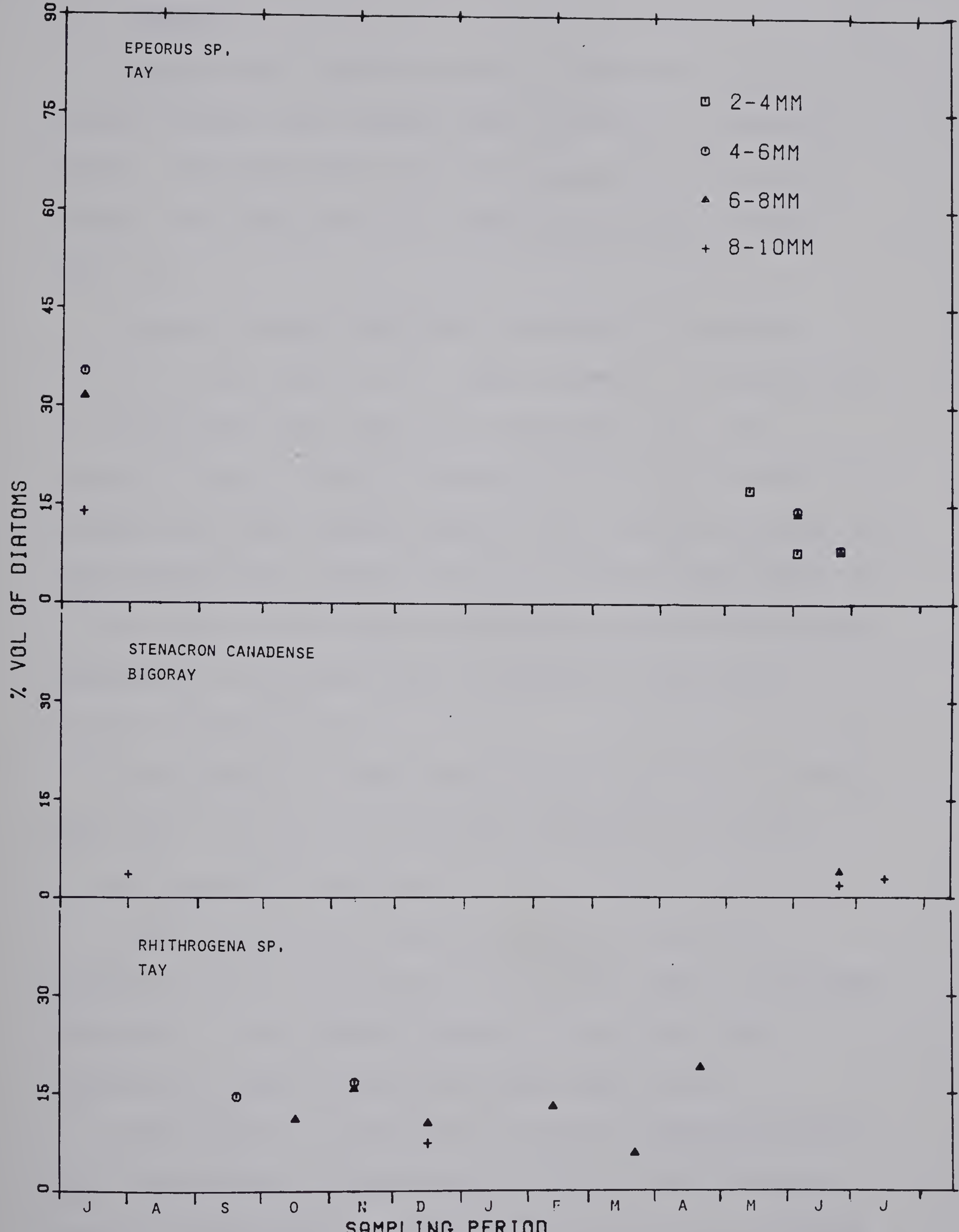

Figure 35. Proportion of ingested material composed of diatoms for the various size classes of <u>Epeorus</u> sp., Tay River; <u>Stenacron</u> <u>canadense</u>, Bigoray River; <u>Rhithrogena</u> sp., Tay River (1975-1976).

Epeorus

Epeorus sp. occurred only in Tay River. It is a summer species with nymphs first evident in the April sample. The population grew very rapidly during the spring, and emergence was completed by early August (Fig. 34).

Epeorus nymphs analyzed contained on average 80 to 85% detritus for all size classes. The proportion of diatoms consumed was quite variable (Fig. 35). Nymphs 4-8 mm in length ingested 30 to 35% diatoms during July 1975. During spring 1976, diatom consumption was considerably lower; levels near 20% in May declined to less than 10% in June. The spring decline in diatom consumption coincided with a decline in epilithic diatom standing crops.

Consumption of sand grains was very low, generally less than 0.5%, and filamentous algae were detected in trace quantity only once.

Total volume of ingested material was below average, with the exception of 2-4 mm nymphs. Specimens collected in the spring generally contained more material in their guts than summer specimens.

The sizes of particles consumed by *Epeorus* nymphs were consistently below average for all size classes, ranging from 76-83% in PSCI. Seasonal trends indicated a slight preference for smaller particles during summer

when compared to spring.

Epeorus nymphs have been reported to ingest from 60% diatoms (Chapman and Demory 1963) to 9% (Shapas and Hilsenhoff 1976), with the average in the range of 25-35%. The increase in detrital ingestion by older nymphs, which I observed, has also been reported by Gilpin and Brusven 1970.

Stenacron

Bigoray River was the only location where *Stenacron interpunctatum canadense* was collected. It appears (Fig. 34) to have a univoltine winter life history. Small nymphs first appeared at the end of July and some autumn growth was evident. There appears to be little if any winter growth. Resumption of growth occurred in the spring, and the last of the old generation emerged by the end of August.

I had material for only four food habit analyses. In all instances, detritus formed greater than 95% of material ingested and diatoms less than 5% (Fig. 35). There were no filamentous algae and animal fragments in the guts, and mineral particles were present in only trace amounts. Total ingested food volume was well above average for all 6-8 and 8-10 mm nymphs examined. Size of particles ingested was close to the study average, with summer specimens consuming an above average number of 32 um or less diameter particles

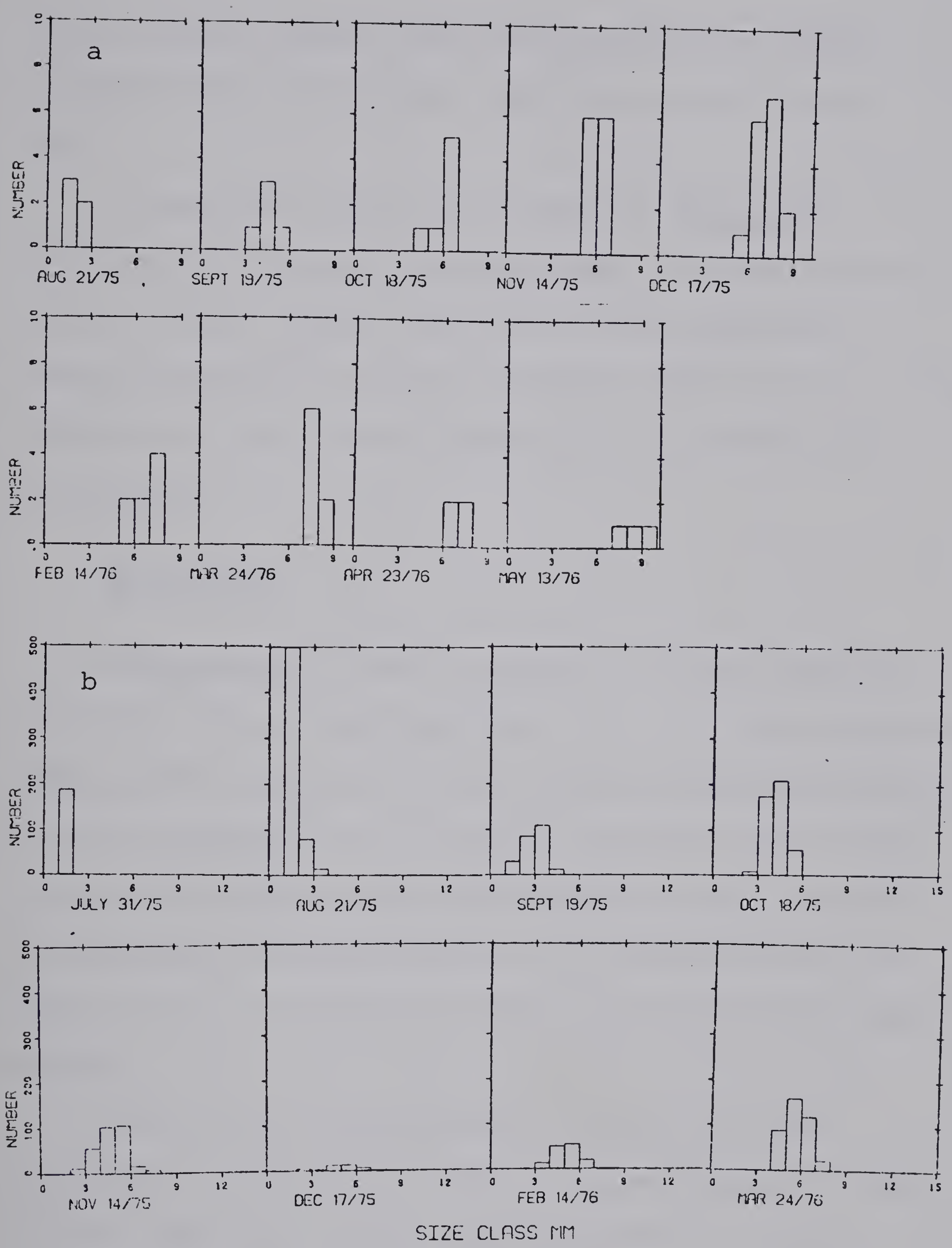

Figure 36. Number of <u>Rhithrogena</u> sp. nymphs per mm size class, Tay River (a); <u>Leptophlebia</u> sp., Stauffer 2 (b).

(72%); whereas during the spring months the nymphs consumed relatively larger particles, only 59% in PSCI.

I found few direct references to Stenacron food habits. However, for Stenonema, a closely related genus, Coffman (1967) reported numerous species to be mostly dependent on algae. Minckley (1963) and Richardson and Tarter (1976) found Stenacron to be primarily a detritivore.

Rhithrogena

Rhithrogena sp. was a univoltine winter species, occurring only in the Tay River (Fig. 36). New generation nymphs first appeared in late August. They grew rapidly during autumn and early winter. The first fully grown nymphs were collected in mid-December. Growth appears to continue throughout winter, with emergence during early spring. No mature specimens were collected after mid-May.

Nymphs from the population studied consumed predominantly detritus, which averaged between 85 and 92% for each size class. The remainder was almost entirely diatoms, composing 5 to 20% of the total material ingested (Fig. 35). No seasonal trends were evident and diatom consumption did not correlate with epilithic standing crops. No food items other than

detritus and diatoms were detected; mineral particles always composed less than 0.5% of the total volume.

Total volume ingested by Rhithrogena nymphs was above average for 4-6 and 6-8 mm specimens and slightly below average for 8-10 mm nymphs. Above average proportions of small particles, 32 um and less in diameter, were consumed by 4-6 and 6-8 mm Rhithrogena nymphs; whereas large 8-10 mm nymphs ingested greater proportions of larger PSCII and III particles.

There are three reports on the food habits of the Palearctic Rhithrogena semicolorata. Diatoms were reported as the dominant food item in two of these studies (Percival and Whitehead 1929, Badcock 1949) and detritus in the other study (Jones 1950). Jones's study was conducted during winter months when epilithic diatoms may have been at low densities. For Nearctic Rhithrogena species, detritus has been indicated as the major food item (Gilpin and Brusven 1970, Shapas and Hilsenhoff 1976), but often with significant quantities of diatoms consumed.

Leptophlebiidae

Leptophlebia

Food habits of Leptophlebia nymphs from Bigoray River and Stauffer 2 were studied. Leptophlebia cupida (Say) was the species collected from the Bigoray River.

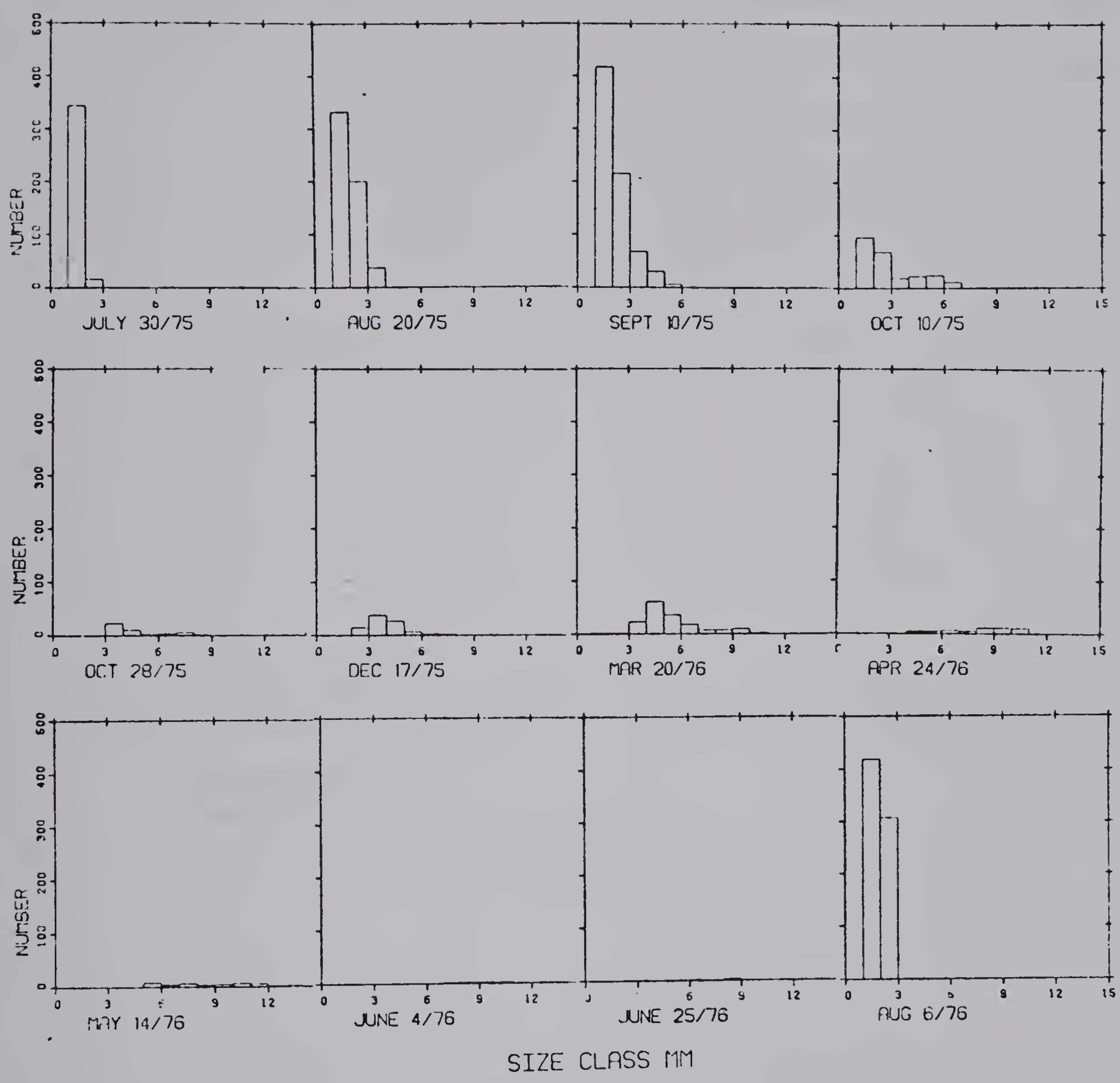

Figure 37. Number of <u>Leptophlebia</u> <u>cupida</u> nymphs per mm size class, Bigoray River.

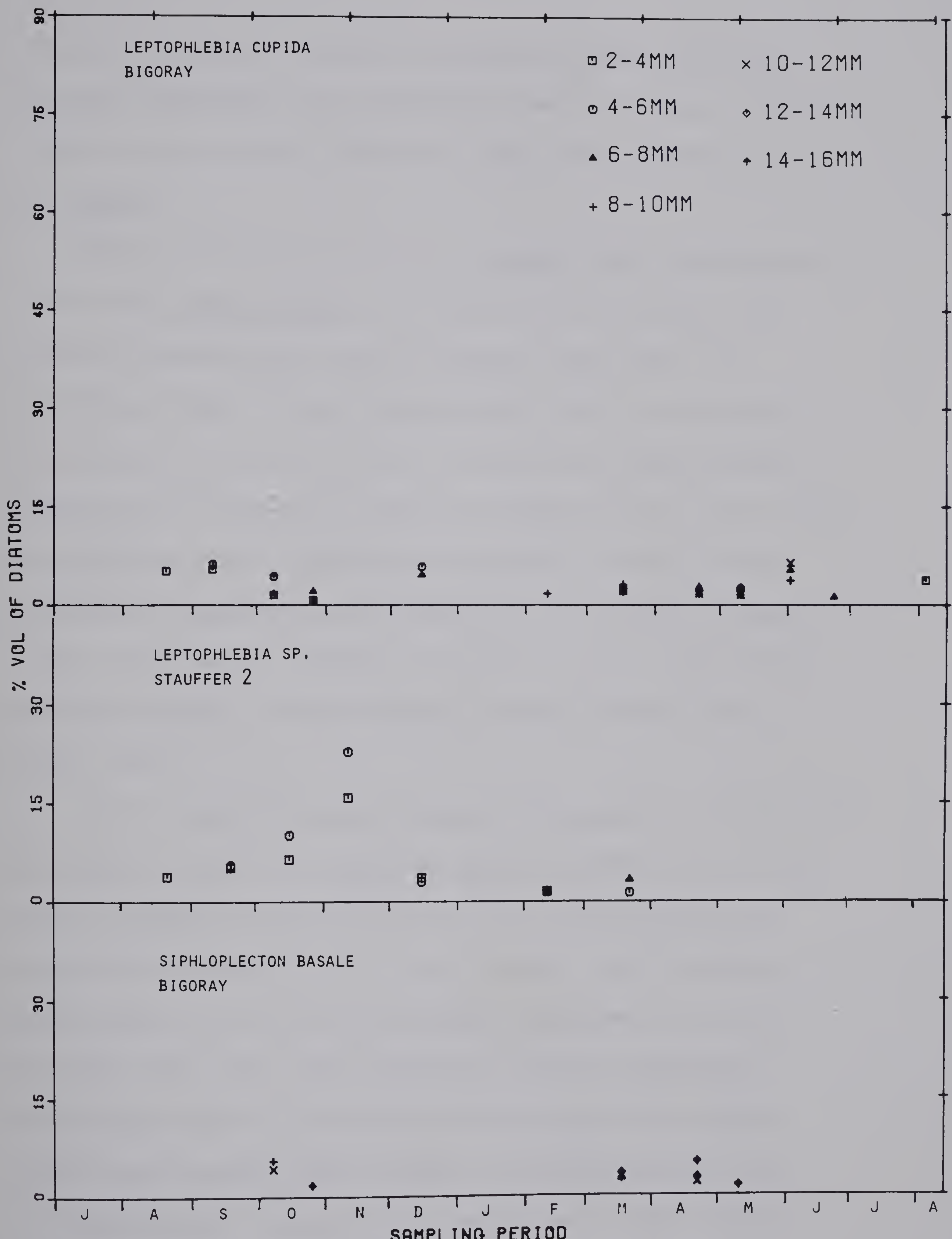

Figure 38. Proportion of ingested material composed of diatoms for the various size classes of *Leptophlebia cupida* Bigoray River; *Leptophlebia* sp., Stauffer 2; *Siphloplecton basale*, Bigoray River (1975-1976).

Adults (which are needed for species identification) were not obtained from Stauffer Creek; however observations on the nymphs indicated they were probably also L. cupida.

The life histories of L. cupida from the Bigoray River and Leptophlebia sp. from Stauffer Creek are those of univoltine winter species (Fig. 36, 37) (Clifford 1969). Young nymphs were first collected at the end of July from both locations. Rapid autumn growth was followed by reduced growth during the winter. The Bigoray River population resumed growth in the spring and emerged during June. The Stauffer 2 population, in contrast, underwent rapid spring growth then either emerged or migrated to another habitat, by early April.

Both populations were mostly dependent on detrital materials. Detritus composed approximately 95% of the total volume on most occasions. The only exception occurred at Stauffer 2 during October and November, when small 2-4 and 4-6 mm nymphs consumed up to 25% diatoms (Fig. 38). This elevated diatom ingestion correlated with an epilithic diatom peak. No other size class trends were evident at either site. The only additional materials ingested were sand grains, which composed up to 2.5% of the total volume, but more frequently occurred at levels below 1.0%.

Average total ingested volumes for all size classes of the Bigoray River population were higher than the study average. Seasonally, the 2-4 and 8-12 mm nymphs' peak consumption occurred during winter; for the 4-8 mm nymphs, the peak was in spring. The Stauffer 2 population had above average yearly ingestion for 2-4 mm nymphs only. Larger nymphs consumed close to average total volumes. Seasonally, peak volumes consumed occurred during autumn for the 2-4 mm nymphs and during late winter for larger size classes.

The size distribution of particles consumed was approximately equal to the study mean for the Stauffer 2 population. The Bigoray River population generally consumed greater proportions of larger PSCII and III diameter particles. Larger *L. cupida* nymphs ingested relatively more large particles. *Leptophlebia* from the Bigoray River contained relatively more PSCI particles during summer, coincident with the first appearance of the new generation. Seasonally, Stauffer 2 specimens ingested more large particles in autumn.

Other food habit studies of *Leptophlebia* nymphs have reported a larger diatom component than found in my study (Brook 1975, Shapas and Hilsenhoff 1977, Moore 1977).

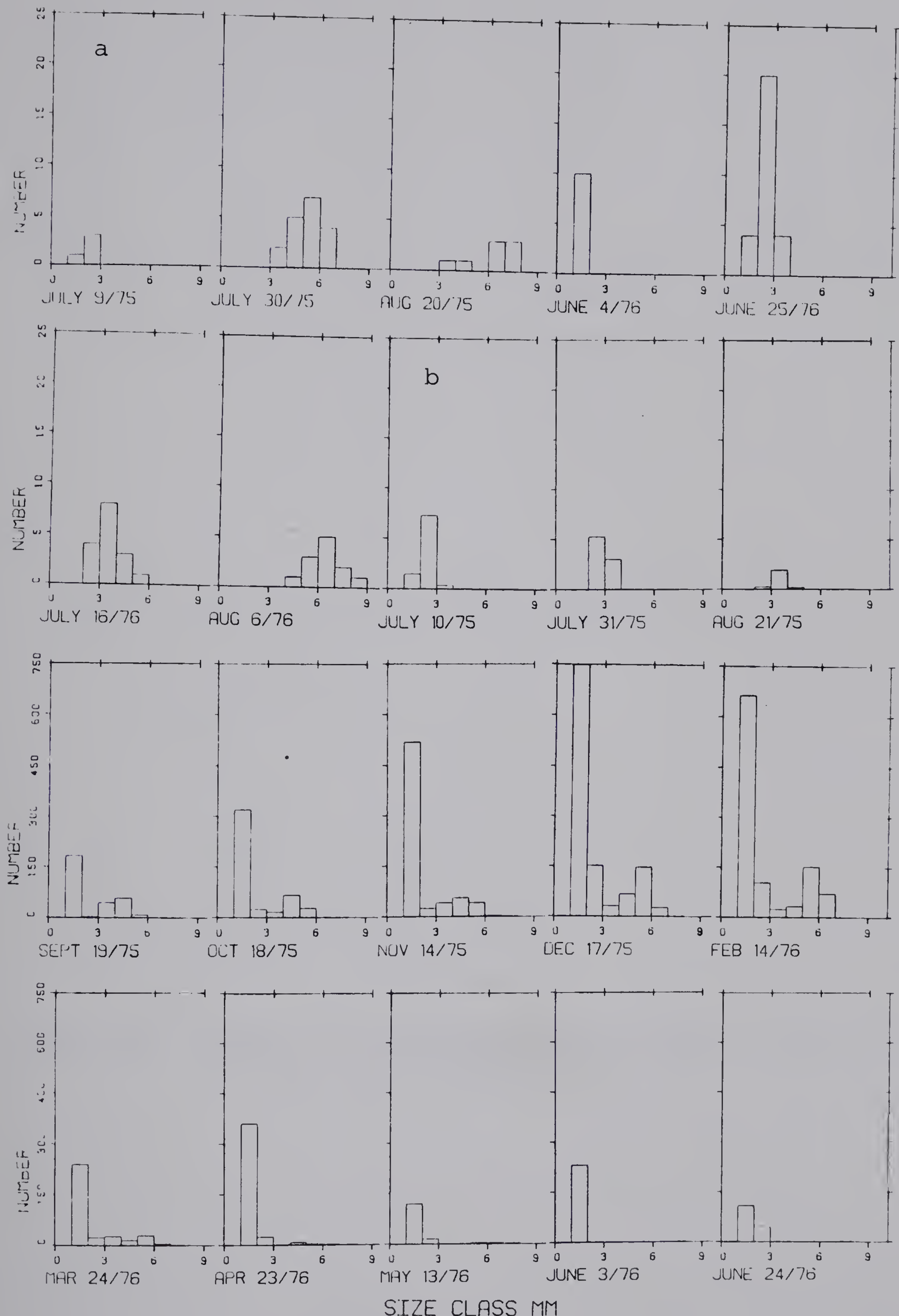

Figure 39. Number of Paraleptophlebia debilis nymphs per mm size class, Bigoray River (a); Paralepto-phlebia sp., Tay River (b).

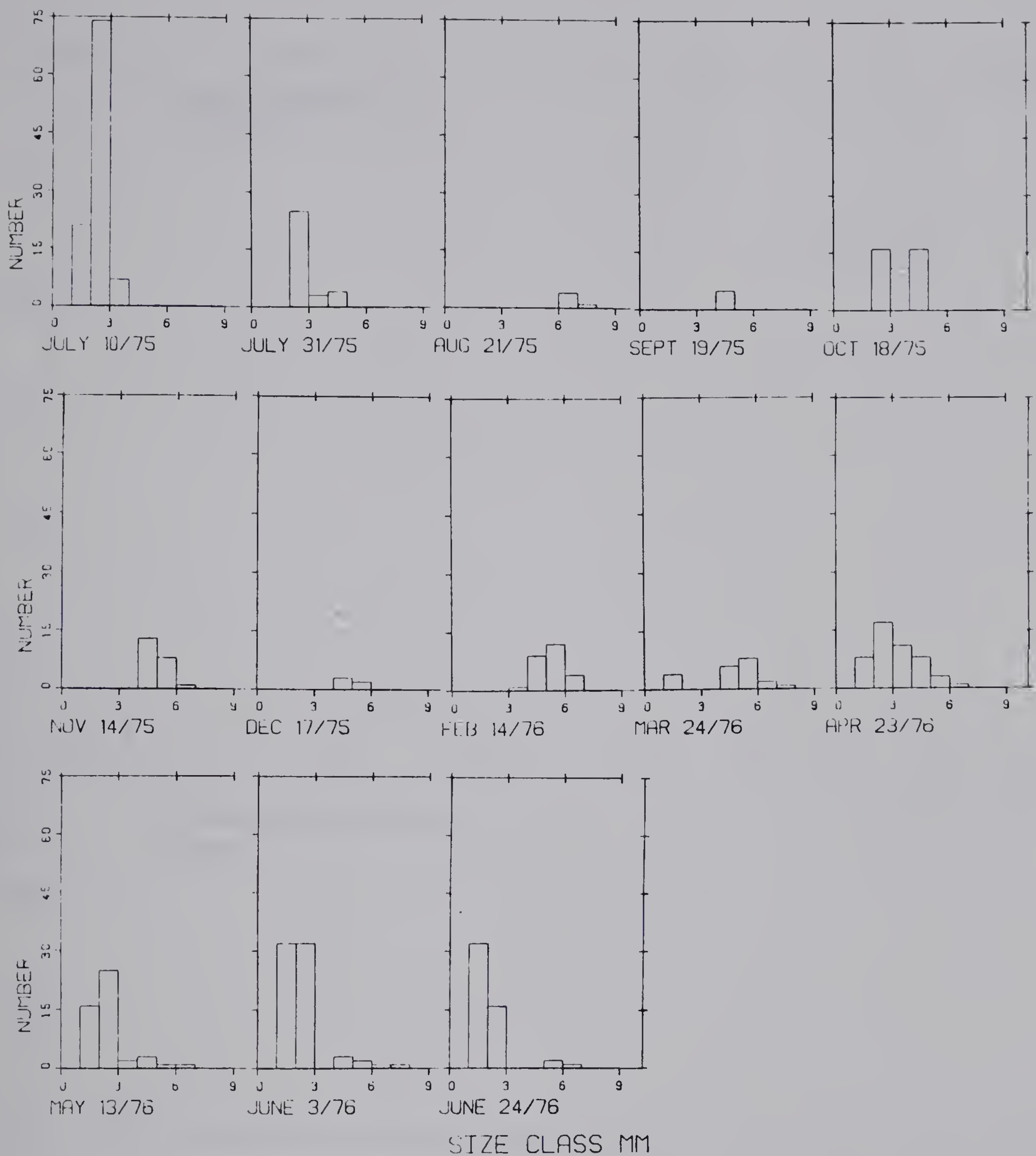

Figure 40. Number of Paraleptophlebia debilis nymphs per mm size class Stauffer 2.

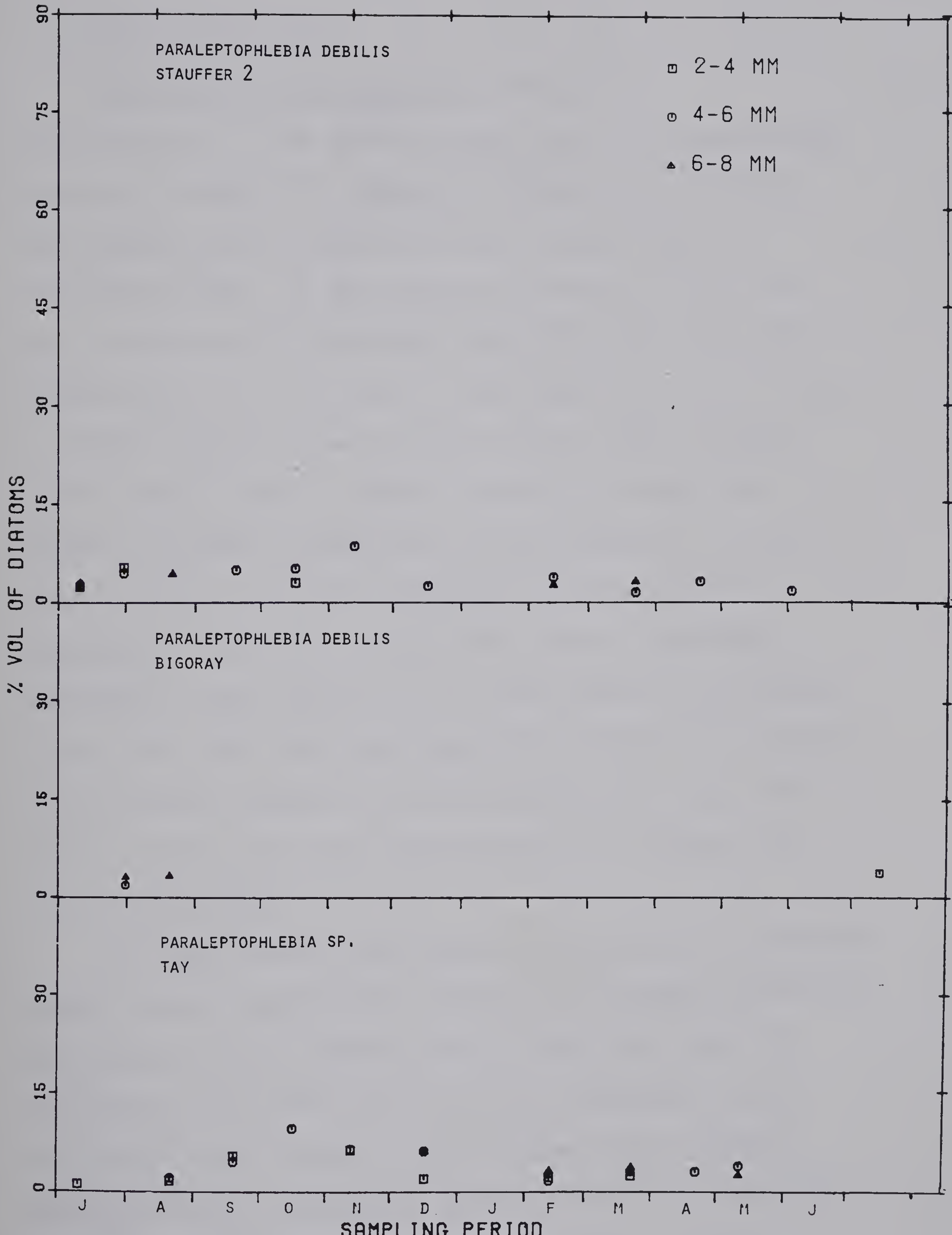

Figure 41. Proportion of ingested material composed of diatoms for the various size classes of <u>Paraleptophlebia debilis</u> Stauffer 2 and Bigoray River; <u>Paraleptophlebia</u> sp., Tay River (1975-1976).

Paraleptophlebia

Paraleptophlebia debilis occurred at both Stauffer 2 and Bigoray River, and an undetermined species (possibly *P. debilis*) occurred in Tay River. The Bigoray River population is a summer species (Clifford 1969). It was first collected in late June and had emerged by September (Fig. 39, 40). The life histories were less clear at the other two sites, where a summer population was evident along with a second winter population or perhaps another species. The summer Stauffer 2 population first appeared in late March and had completed emergence by the end of September. The winter population started hatching in September, grew through autumn and winter, and emerged in May and June. The Tay River population had a similar life history pattern, with the possibility that some summer nymphs may have overwintered and emerged the following spring.

All populations were heavily dependent on detritus, which always composed 90% or more of ingested materials. The Bigoray River population consumed less than 4% diatoms on all dates (Fig. 41). For Stauffer 2 and Tay River, the 2-4 and 4-6 mm classes had slightly elevated diatom ingestions during autumn, correlating with epilithic diatom peaks at this time. Diatom ingestion then declined and detritus completely dominated

the food habits during late winter and spring. Little size class variation of ingestion patterns occurred in any of the populations.

The only other material ingested was mineral particles, which varied between 0.2 and 2.0% of the total ingested volume.

Total volume of consumed material was substantially above the study average for Bigoray River specimens. Similarly, all nymphs except those of the 6-8 mm size class consumed above average volumes at Stauffer 2. Peak volumes were ingested by 4-6 mm Stauffer 2 nymphs during spring. The Tay River population consumed slightly below average total volumes for all size classes. Seasonally, 4-6 mm nymphs consumed peak quantities in spring and lowest volumes during summer and early winter. Peak consumption for 6-8 mm nymphs occurred in winter.

Paraleptophlebia nymphs of all size classes and at all sites consumed average or above average volumes of small PSCI particles; this trend was most apparent in the Tay River population. No seasonal trends in size of consumed particles were evident for Bigoray River nymphs; however, at Stauffer 2, the greatest proportion of small particles were consumed in winter, and the smallest in spring.

Most investigators report *Paraleptophlebia* as

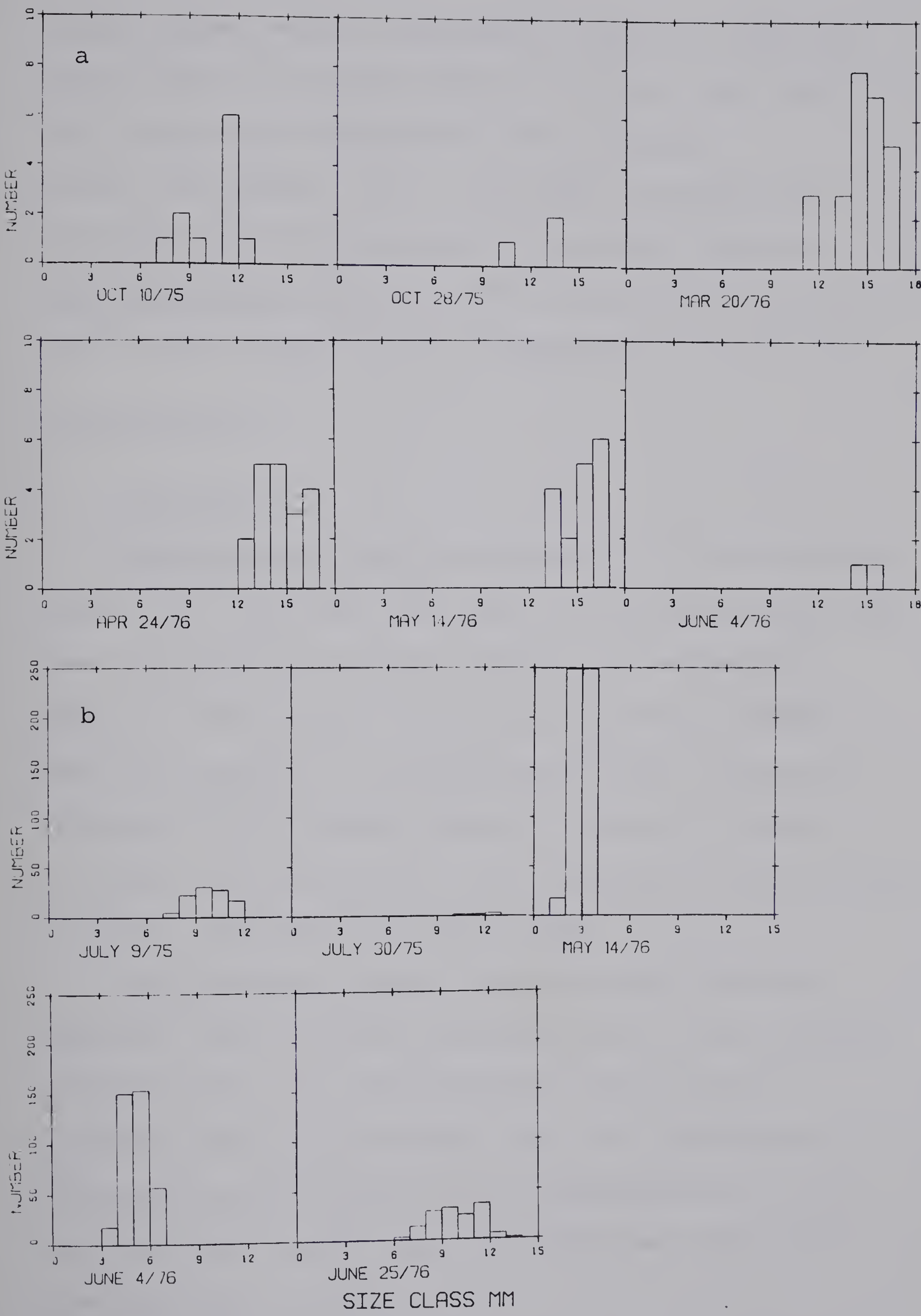

Figure 42. Number of Siphloplecton basale nymphs per mm size class (a); and Siphlonurus alternatus (b) from Bigoray River.

eating almost entirely detritus, this food composing 90% or more of consumed material (Chapman and Demory 1963, Shapas and Hilsenhoff 1976). However, Gilpin and Brusven (1970) reported *P. bicornuta* as consuming up to 27% diatoms. All workers indicate *Paraleptophlebia* species prefer interstitial habitats, which would coincide with the dependence on detritus.

Metretopodidae

Siphloplecton

Siphloplecton basale occurred only in the Bigoray River (Fig. 42). The life cycle of this population has been described by Clifford (1976) as a univoltine species. Young nymphs first appeared during summer; they grew rapidly (0.8 mm per week) until freeze-up (Clifford 1976). Growth ceased or was much reduced in winter, and there was little increase in total length in spring. Emergence started in May.

Siphloplecton basale ingested almost entirely detritus, diatoms seldom exceeding 5% of total stomach contents (Fig. 38). No appreciable size class or seasonal trends were evident. The only other material consumed was sand grains, which composed up to 3% of the total gut volume. This was high when compared to other species studied.

Total volume of gut material was above average for all size classes, with peak consumption during

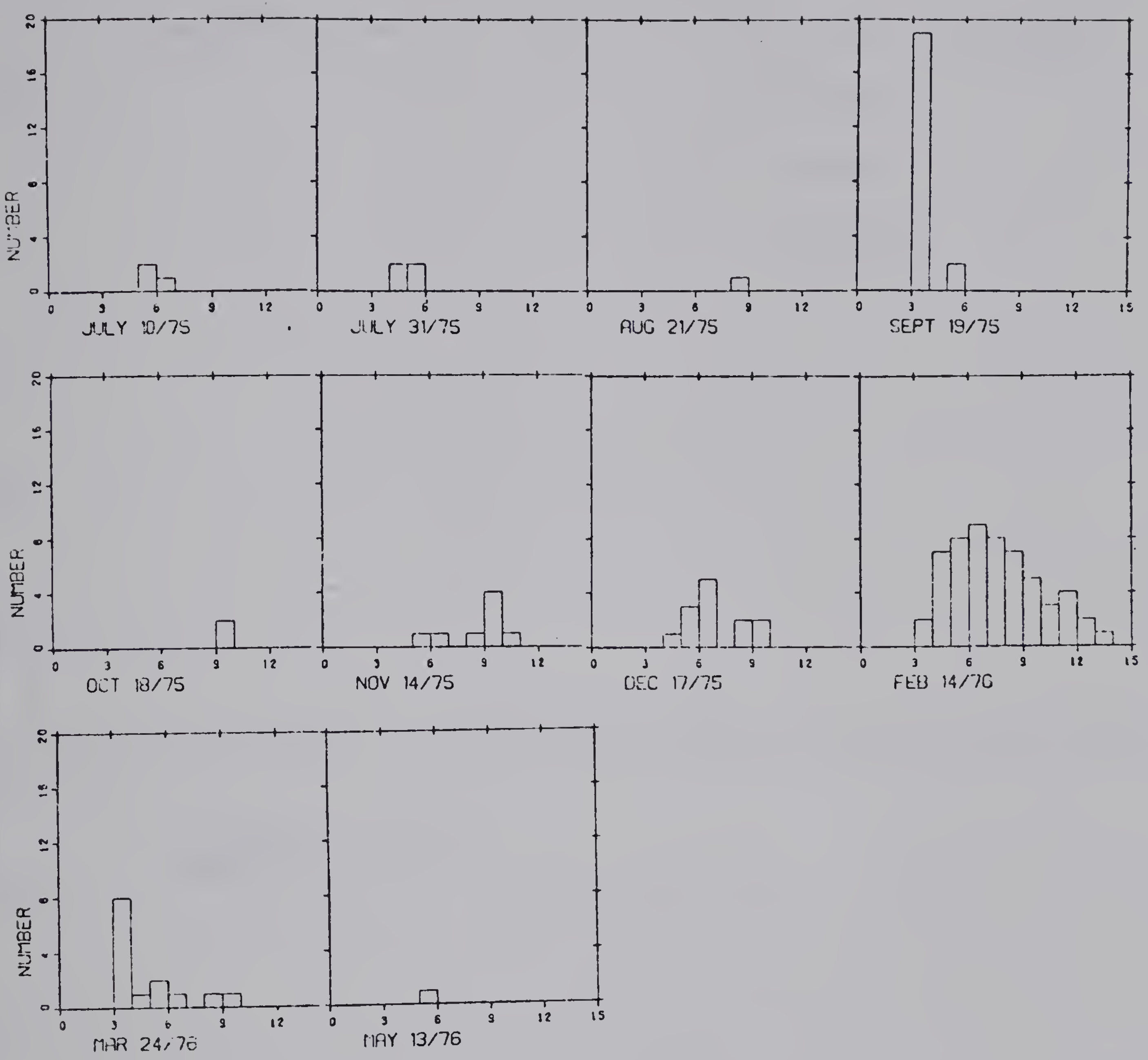

Figure 43. Number of <u>Ameletus sparsatus</u> nymphs per mm size class, Bigoray River.

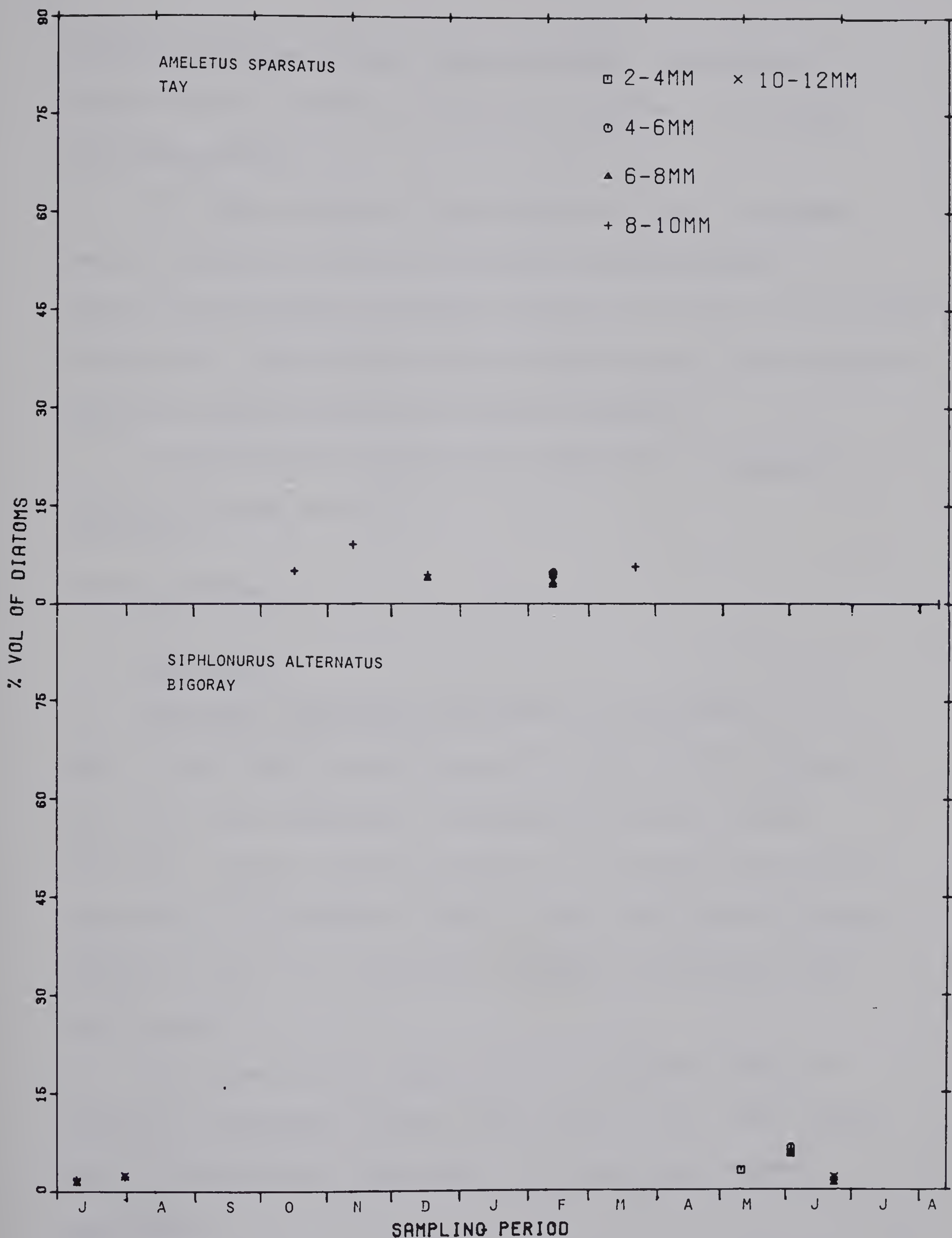

Figure 44. Proportion of ingested material composed of diatoms for the various size classes of Ameletus sparsatus nymphs, Tay River and Siphlonurus alternatus, Bigoray River (1975-1976).

winter. For the largest size classes, a decline in total volume ingested occurred in spring, coincident with emergence.

All size classes (especially 8-12 mm) consumed below average volumes of 32 um or less diameter particles and above average volumes of 32-64 um particles. Seasonally, the pattern was uniform except for a slight shift to smaller particles during spring.

I could find no previous references to _Siphlo-plecton_'s food habits.

Siphlonuridae

Ameletus

Ameletus sparsatus occurred in Tay River. Due to the small sample sizes I could not determine its life cycle pattern. It appears to be a winter species; nymphs hatching during late August and early September, followed by rapid autumn and spring growth phases (Fig, 43). Emergence probably continued into mid-August.

The species was dependent on detritus (90% of volume) throughout autumn and winter (Fig. 44). There were insufficient specimens for spring and summer analyses.

Volume consumed was below average for all size classes, particularly for the largest nymphs (12-14 mm).

Total consumption was lowest in autumn and highest in winter.

Size of consumed particles was average or slightly below for most size classes, and seasonally there was a relatively slight increase in ingestion of small particles in winter.

Gilpin and Brusven (1970) report *Ameletus* nymphs consumed 60-85% detritus. Similarly, Muttkowski and Smith (1929) found *Ameletus* specimens consuming between 50-98% detritus.

Siphlonurus

Siphlonurus alternatus was a summer species collected only from the Bigoray River. The new generation first appeared in early May; the nymphs grew very rapidly throughout spring and emerged in July (Fig. 42).

The primary diet component was detritus, which composed greater than 90% of the total stomach contents on all occasions. Highest percent diatom ingestion occurred on 4 June 1976, correlated with a peak standing crop of epilithic diatoms at this time in the Bigoray River (Fig. 44).

Siphlonurus alternatus nymphs except for the 2-4 mm size class, consumed very large total volumes of material.

Nymphs up to 6 mm in length consumed above average

quantities of small particles. Larger nymphs consumed relatively more large particles (PSCII and III). Seasonally, more small particles were consumed during spring than in summer.

The diet of Siphlonurus nymphs has been reported to vary from almost complete reliance on detritus (Jones 1950, Shapas and Hilsenhoff 1976) to more of an omnivorous nature with facultative animal ingestion if detritus and diatoms were not available (Edmunds 1960).

Analysis of Diatoms Consumed

Relative abundance of diatoms ingested by each mayfly taxon was initially difficult to analyze because of the large number of guts analyzed and the diversity of diatom species encountered. This problem was overcome by use of multivariate statistical methods, namely cluster analysis and principal component analysis. Cluster analysis is a technique whereby the mayfly species analyzed could be placed into groups (clusters) based upon similarities amongst the diatom species and relative abundances of diatoms ingested. Principal component analysis (PCA) was then utilized to distinguish the diatom species which were most important in defining each cluster. Details of these techniques are generally described by Lee (1971), Sneath and Sokal (1973),

Table 18. Percent composition of ingested diatoms - Stauffer 2, 10 July 1975.

Species	Size Class	Fragilaria leptostauron	Fragilaria lepto-stauron var. dubia	Navicula Sp. A	Cocconeis placentula	Fragilaria construens	Achnanthes sp.	Nitzchia Sp. B	Other Species	Navicula viridula	Navicula cryptocephala
Baetis spp.	2-4	1.3	1.8	0.9	83.9	5.4	0.9	0.0	0.0	2.7	0.9
	4-6	4.0	0.6	0.6	75.6	4.3	3.2	0.0	0.9	5.2	3.2
	6-8	2.3	0.3	0.3	78.4	3.7	0.7	1.0	1.3	4.7	4.7
Cinygmula mimus	4-6	1.5	3.0	0.8	33.3	19.7	11.4	3.8	6.1	5.3	8.3
	6-8	11.2	9.6	5.6	36.0	8.8	4.0	0.0	8.0	6.4	1.6
Ephemera simulans	4-6	9.5	19.0	0.0	27.6	27.6	6.0	0.0	5.2	3.4	0.0
	6-8	12.0	9.8	0.8	21.8	36.1	6.0	0.8	3.8	6.0	0.0
	8-10	12.9	27.3	0.8	15.9	22.0	4.5	3.0	6.1	4.5	0.8
Ephemerella inermis	4-6	5.5	2.2	0.0	65.6	6.6	6.6	0.0	3.8	4.9	0.0
	6-8	8.5	1.5	1.0	59.5	13.0	0.5	0.5	5.0	4.5	2.0
Paraleptophlebia debilis	2-4	17.5	6.3	3.2	36.5	25.4	4.8	0.0	3.2	1.6	1.6
	4-6	13.2	9.9	0.8	34.7	14.9	4.1	1.7	7.4	7.4	1.7
	6-8	12.9	10.6	3.5	29.4	20.0	8.2	0.0	7.1	2.4	1.2

Clifford and Stephenson (1975), and Boland (1976). The application of these techniques to aquatic communities include studies by Roback et.al. (1969), de March (1976), Boland (1976) and Sprules (1977).

Cluster analysis and principal component analysis were carried out for the stomach samples of each site for one sampling date each season. Ingested diatoms were analyzed separately for each site due to possible differences in diatom availability between sampling locations. It was not feasible to analyze stomach samples from more than one sampling date at one time, because seasonal changes in available diatom composition could mask any differential ingestion of diatom species. Sampling dates on which multivariate analysis were done often varied between sites; this was necessary to maximize the number of species and size classes that could be included in each analysis.

I used the multivariate analysis program entitled Clustan (Wishart 1975) for both cluster analysis and PCA. Data from Stauffer 2 on 10 July 1975 will be used as an example of my procedure (Table 18). Data entered the computer as a matrix with rows representing size classes of mayfly species (e.g. Baetis 2-4 mm) and columns representing proportional abundances of diatom species from the guts of each size class. Diatom species that did not account for 3% of the total number of diatoms consumed by at least one nymphal size class

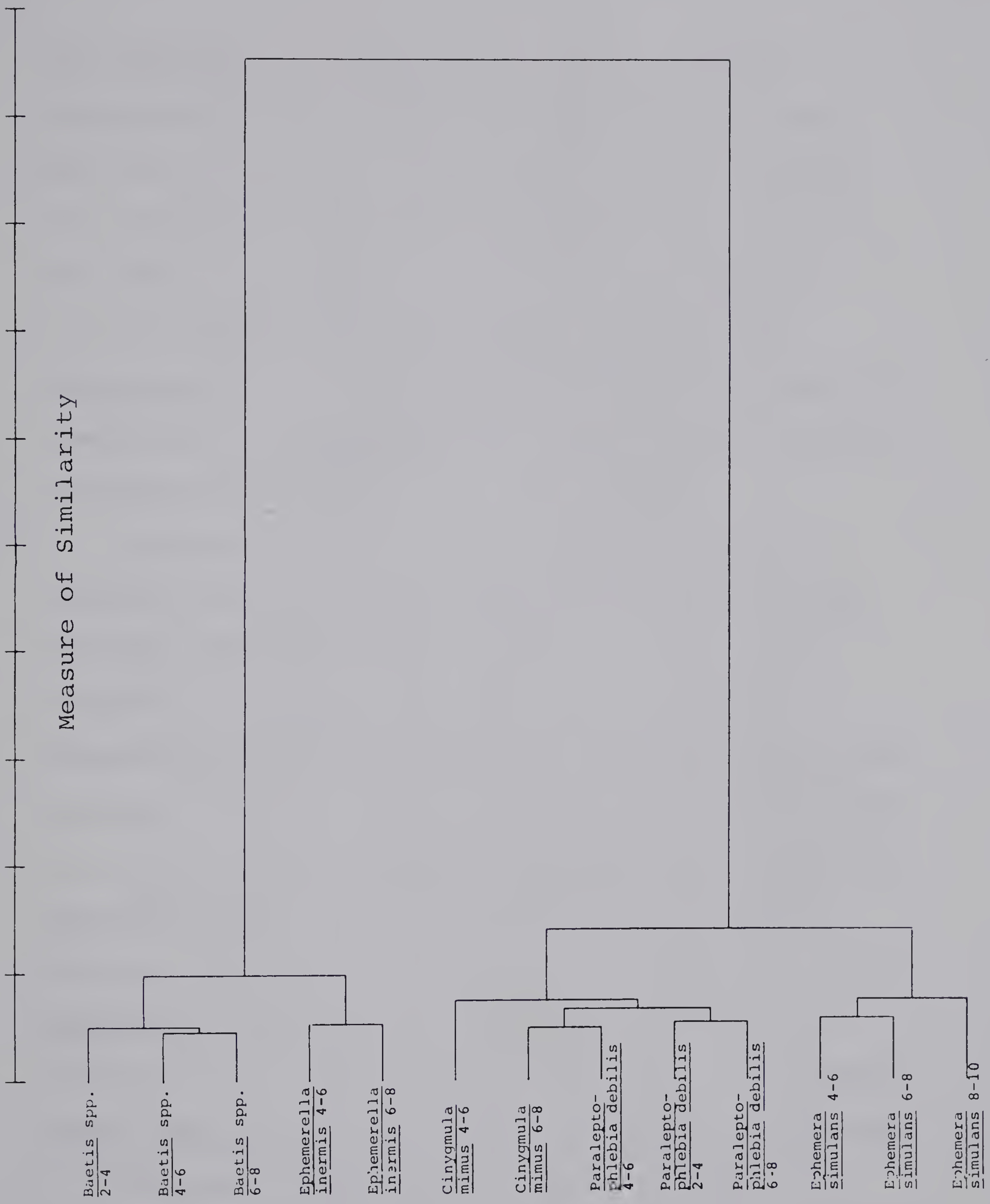

Figure 45. Cluster analysis dendrogram based on diatoms ingested by each mayfly size class analyzed on 10 July 1975 at Stauffer 2.

were excluded to increase normality of the data. Proportionate data rather than absolute cell counts were used to prevent clustering of samples based on the quantity of each diatom consumed rather than on its relative abundance (Clark 1976). For example, a 4-6 mm *Baetis* nymph may consume twice as many *Achnanthes* as a 2-4 mm specimen; however, the relative composition of *Achnanthes* with respect to all diatoms consumed may be similar for both samples.

Cluster analysis consisted of calculating a similarity matrix between samples using the Squared Euclidean Distance Method (Sneath and Sokal 1973). Clustering of samples was then done using Ward's Hierarchical Fusion Method (Ward 1963). The clustering procedure results in the construction of a dendrogram (Fig. 45). For the Stauffer 2 example, the clustering procedure defined two major groups of gut samples. Diatoms contained in the guts of all *Baetis* spp. and *Ephemerella inermis* size classes were similar and distinct from diatoms present in the guts of *Cinygmula mimus*, *Paraleptophlebia debilis* and *Ephemera simulans*.

Principal component analysis on the same data involved calculation of a correlation matrix from which eigenvalues and eigenvectors were in turn derived. Eigenvalues and eigenvectors summarize any variation in diatoms consumed in a more condensed form than the

Table 19. Principal components analysis of ingested diatoms for Stauffer 2 gut samples 10 July 1975.

Eigenvalue	% Variance	Eigenvectors: *Fragilaria leptostauron*	*Fragilaria lepto-stauron* var. *dubia*	*Navicula* Sp. A	*Cocconeis placentula*	*Fragilaria construens*	*Achnanthes* spp.	*Nitzchia* Sp. B	Other Species	*Navicula viridula*	*Navicula cryptocephala*
4.08	40.80	0.39	0.39	0.17	-0.49	0.39	0.28	0.15	0.39	0.03	-0.13
2.26	22.62	-0.32	-0.07	-0.23	-0.07	-0.03	0.32	0.57	0.13	0.33	0.54
1.26	12.57	0.10	-0.25	0.69	0.04	-0.37	-0.04	-0.14	0.40	0.32	0.18
1.07	10.72	0.05	0.26	-0.30	0.01	-0.16	-0.46	0.09	0.12	0.68	-0.34
0.55	5.49	-0.08	-0.42	-0.21	-0.00	0.22	0.54	-0.45	0.03	0.40	-0.27
0.41	4.10	-0.42	0.44	-0.06	0.09	-0.50	0.38	-0.09	0.30	-0.21	-0.29
0.18	1.80	0.47	-0.34	-0.48	0.14	-0.23	-0.03	0.08	0.51	-0.29	0.01
0.12	1.16	-0.50	-0.02	-0.09	-0.10	0.39	-0.40	-0.32	0.52	-0.12	0.19
0.07	0.72	-0.27	-0.40	0.23	0.06	0.17	-0.08	0.55	0.12	-0.12	-0.59
0.00	0.00	0.12	0.26	0.11	0.84	0.37	0.12	0.06	0.15	0.08	0.05

raw data matrix. The first ten eigenvectors (rows), with corresponding eigenvalues, for this example are presented in Table 19.

The proportion of the total variance in the data that can be explained by each eigenvector is derived from the eigenvalue. The first eigenvector of the Stauffer example accounts for 40.8% of the total variance in diatom ingestion, the second 22.62%, and the third 12.57%. Each successive eigenvector accounts for a lesser portion of the total variance. The first two eigenvectors usually explain most of the data variance; therefore they are the only ones analyzed.

Individual values of an eigenvector indicate the importance of each diatom species in accounting for the proportion of the variance explained by that eigenvector. For vector 1 in the example, Fragilaria construens, F. leptostauron var. dubia, F. leptostauron and Achnanthes spp. had high positive correlations with component one, while Cocconeis placentula had a high negative correlation. A bivariate plot can be produced indicating the location of each stomach sample included in the analysis with respect to the first two principal components. Position of a stomach sample is determined by calculating its factor scores from the first and second eigenvectors. A factor score is a sum of the

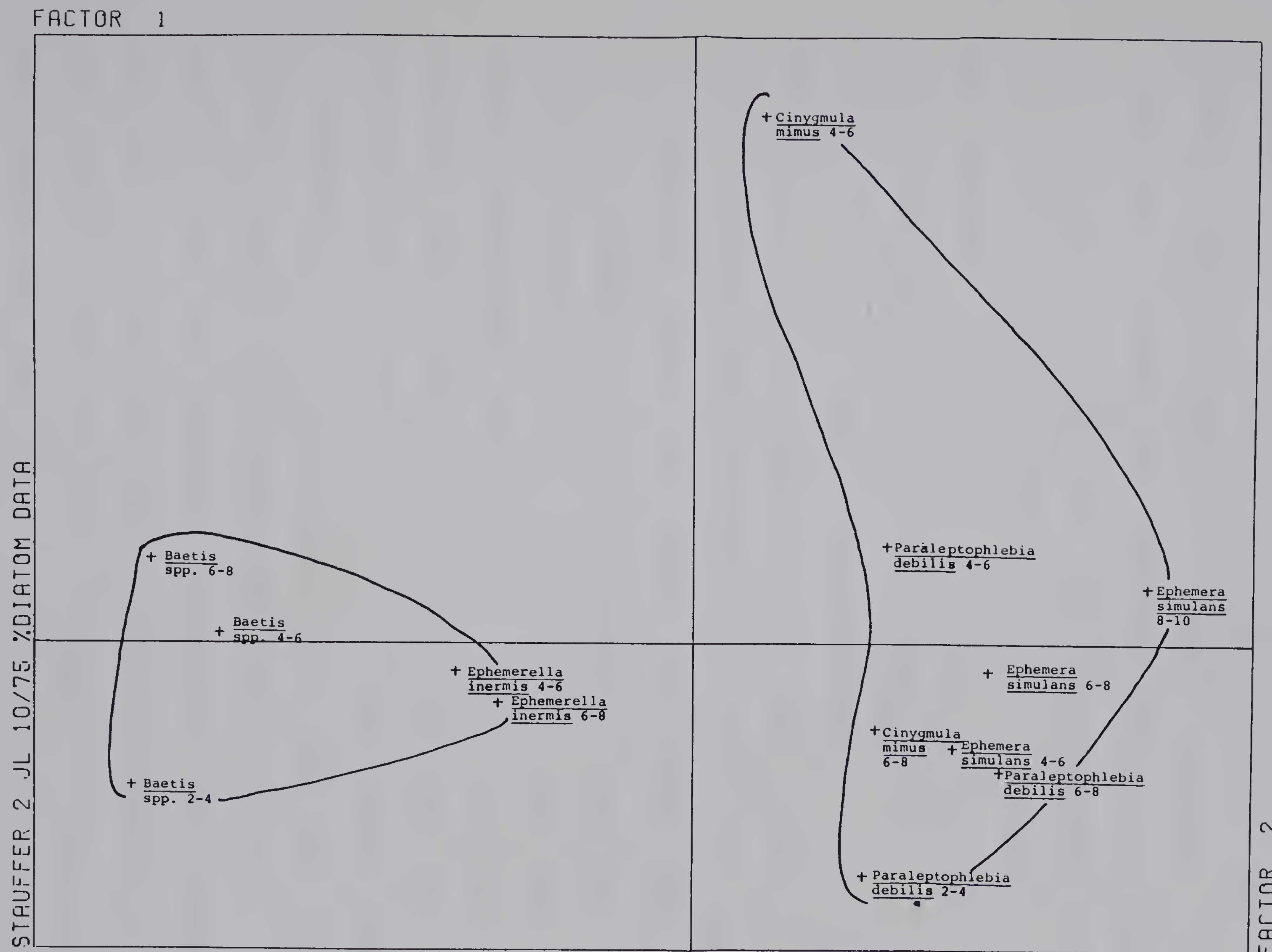

Figure 46. First two principal components with location of each gut sample analyzed with respect to each component indicated - 10 July 1975 data from Stauffer 2.

proportionate abundances of each diatom species in the stomach sample times their corresponding component coefficient in the eigenvector. The plot for the example indicates the first principal component to be along the horizontal axis and the second to be along the vertical axis (Fig. 46). The two components intersect at 0 with increasing positive values on one side of the intersection and negative values on the other side. The position of the 6-8 mm Baetis nymphs in the example indicates a large negative factor score for the first principal component and a small positive factor score on the second principal component. From this position, it can be inferred that diatom species with high negative values in eigenvector one were ingested by 6-8 mm Baetis spp. in high proportions, while diatoms with high positive values were not. A positive factor score for principal component two indicates that the positively correlated diatom species in eigenvector two were slightly more important. The stomach samples are grouped along factor one in a similar fashion to groupings produced by the cluster analysis. Clusters from the cluster dendrogram have been superimposed on the bivariate plot to compensate for distortions resulting from a change in dimensionality in the PCA (Sprules 1977).

In summary, the first principal component accounts

Table 20. PC analysis summary of ingested diatoms for various size classes of nymphs, Stauffer 1.

	30 July, 1975		14 November, 1975		14 February, 1976		23 April, 1976	
GROUP 1	*Cinygmula mimus*	6-8	*Cinygmula mimus*	2-4	*Cinygmula mimus*	4-6	*Cinygmula mimus*	4-6
Surface Feeders		8-10			*Baetis* spp.	2-4		6-8
	Baetis spp.	2-4			*Cinygmula mimus*	2-4	*Baetis* spp.	6-8
		4-6						
GROUP 2	*Baetis* spp.	6-8	*Baetis* spp.	4-6	*Baetis* spp.	4-6	*Baetis* spp.	2-4
Interstitial Feeders	*Ephemerella tibialis*	4-6		2-4	*Ephemerella inermis*	6-8		4-6
		6-8	*Ephemerella inermis*	4-6		4-6	*Ephemerella inermis*	8-10
			Ephemerella tibialis	6-8				6-8
GROUP 3			*Ephemerella spinifera*	6-8	*Baetis* spp.	2-4	*Ephemerella spinifera*	10-12
Fluctuating								

Table 21. Relevant diatom taxa defining ingestion clusters of Stauffer 1 mayflies, see text for further explanation.

	30 July, 1975	14 November, 1975	14 February, 1976	23 April, 1976
GROUP 1	*Achnanthes* spp. *	*Cocconeis placentula* *	*Cocconeis placentula* *	*Cymbella sinuata* *
Surface Feeders	*Cocconeis placentula* *	*Achnanthes* spp. *	*Cymbella sinuata* *	*Cocconeis placentula* *
	Synedra sp. *	*Cymbella sinuata* *	*Achnanthes* spp. *	*Achnanthes* spp. *
			Synedra sp. A *	
GROUP 2	*Fragilaria construens* +	*Fragilaria leptostauron* +	*Fragilaria leptostauron* +	*Fragilaria construens* +
Interstitial Feeders	*Fragilaria leptostauron* var. *dubia* +	*Fragilaria leptostauron* var. *dubia* +	Other species	*Fragilaria leptostauron* +
	Fragilaria leptostauron +	*Fragilaria construens* +	*Fragilaria construens* +	
	Other species		*Navicula* sp. B +	
			Fragilaria pinnata	
GROUP 3		*Navicula* sp. B +	*Fragilaria leptostauron* var. *dubia* +	*Navicula* sp. B +
Fluctuating		*Nitzchia* sp. A +	*Synedra* sp. A *	*Fragilaria leptostauron* +
		Cymbella cymbiformis +	Other species	
			Fragilaria leptostauron +	

* Epilithic species

\+ Epipelic species

for the majority of the variance in diatoms ingested. This first component, along with the cluster analysis, divides the mayflies into two groups. One group includes all *Baetis* spp. and *Ephemerella inermis* stomach samples and is characterized by a high ingestion of *C. placentula*. The other group contains the remaining species and is characterized by a lack of *C. placentula* and an abundance of *Fragilaria construens*, *F. leptostauron* and *F. leptostauron* var. *dubia* in the guts. The second principal component further separates 4-6 mm *Cinygmula mimus* nymphs from the latter group; this is due to a relatively greater ingestion of *Nitzchia* B, *Navicula cryptocephala*, *N. viridula* and *Achnanthes* spp. than other group members of diatoms.

Bivariate plots of the other 15 multivariate analyses are presented in the Appendix. A general trend evident in all analyses is for clustering of two main groups of stomach samples, with occasional subdivision of a third.

The major clusters for dates analyzed from Stauffer 1 are summarized in Table 20. The diatoms that were most critical in defining each corresponding group are presented in Table 21. When the significant diatoms of each major group are analyzed for all seasons a uniformity of diatom types is detected. General trends in size classes and species of ephemeropterans that

Table 22. Literature based classification of diatoms.

	Round 1974	Douglas 1958	Blum 1960	Gumtow 1955	Moore 1976	Hynes 1972	Round 1965	Hutchinson 1975	Furnell 1977
EPILITHIC									
Cocconeis placentula	+	+		+	+				
Gomphonema spp.	+	+	+						
Cymbella spp. (stalked)	+			+				+	
Achnanthes spp.	+	+						+	
Cymbella sinuata	+								
Diatoma heimale	+			+					
Meridion circulare	+								
Synedra spp.	+								
Epithemia spp.	+								
Diatoma vulgare					+		+		
EPIPELIC									
Nitzchia spp.	+		+		+	+		+	+
Navicula spp.	+					+		+	+
Gyrosigma spp.	+					+		+	
Surirella spp.	+				+	+			
Diatoma vulgare			+						
Cymatopleura spp.	+						+		
Meridion circulare	+								+

Table 22. (continued).

	Round 1974	Douglas 1958	Blum 1960	Gumtow 1955	Moore 1976	Hynes 1972	Round 1965	Hutchinson 1975	Furnell 1977
Fragilaria leptostauron	+								
Fragilaria construens	+								+
Navicula cryptocephala	+								+
Diploneis spp.	+							+	
Stauroneis spp.	+								
Amphora spp.	+								
Cymbella spp.	+								
Synedra amphicephala									+
Cyclotella spp.								+	
Navicula viridula	+				+				
Nitzchia palea					+				+
Rhoicosphenia curvata					+				
Fragilaria pinnata							+		

occur in each group can also be detected; however more seasonal variability occurs than with the diatoms.

Several workers have indicated that diatoms are relatively specific in their microhabitat selection. Although more work is needed in this area, major microhabitat partitions of some common stream diatom species have been determined (Blum 1960, Round 1964). The major substrate habitats of diatoms in streams have been defined as epilithic (stony substrate), epipelic (depositional substrate type) and epiphytic (attached to other plant material) (Hynes 1972). Table 22 summarizes known microhabitat preferences of benthic stream diatoms relevant to my study. Only epilithic and epipelic diatoms were considered because most sampling was done in areas where these substrates predominate. A species is recorded as epipelic or epilithic if it achieves greatest relative abundance on that habitat type. Most species will likely be found incidentally in other habitats as well (Hutchinson 1975).

When diatom species characteristic of Group 1 are compared with the habitat preference list, most of the frequently occurring species were considered epilithic; for example, _Cocconeis placentula_, _Achnanthes_ spp., _Cymbella sinuata_, _Synedra_ sp. Representatives of Group 2 are predominantly epipelic, e.g. _Fragilaria leptostauron_,

F. leptostauron var. *dubia*, *F. construens* and *Navicula* sp. Representatives of Group 3 are not as closely defined although there appears to be a preponderance of epipelic species in this group.

The substrate at Stauffer 1 consists of surface gravels underlain by sand and silt. Microhabitat partitioning by diatoms on this substrate type would include predominantly epilithic species on exposed surfaces of rocks, with greater abundance of epipelic species inhabiting the interstices where current is reduced and depositional material accumulates. This is likely not a rigid partitioning as evidenced by the relatively high abundance of some epipelic species (*F. leptostauron*, *F. construens*) in the rock scrape samples. These epipelic species may have been most abundant on the lower sides of the rocks, and hence would not be exposed to the current. I could not be certain of this because the epilithic diatom samples that I collected were from entire rock scrapes.

If the dominant type of diatom ingested (epilithic or epipelic) is known, it is therefore possible to predict where on the substrate the nymphs in question are feeding. Mayflies that are members of Group 1 can be considered to feed in areas where epilithic diatoms are most abundant, which would include areas of high current velocity such as upper rock surfaces.

Table 23. PC analysis summary of ingested diatoms for various size classes of nymphs, Stauffer 2.

	30 July, 1975		18 October, 1975		14 February, 1976		23 April, 1976	
GROUP 1	Baetis spp.	2-4	Baetis spp.	2-4	Paraleptophlebia debilis	4-6	Baetis spp.	2-4
Surface Feeders		6-8	Ephemerella inermis	4-6	Baetis spp.	2-4	Cinygmula mimus	4-6
		4-6	Leptophlebia sp.	2-4	Leptophlebia spp.	4-6		2-4
	Ephemerella inermis	4-6	Ephemerella inermis	2-4		6-8		6-8
		6-8	Leptophlebia sp.	4-6			Baetis spp.	4-6
							Ephemerella spinifera spinifera	10-12
							Ephemera simulans	2-4
							Paraleptophlebia debilis	4-6
GROUP 2	Cinygmula mimus	4-6	Paraleptophlebia debilis	4-6	Leptophlebia spp.	2-4	Ephemerella spinifera	8-10
Interstitial Feeders	Paraleptophlebia debilis	2-4	Ephemera simulans	16-18	Ephemerella inermis	4-6	Ephemerella inermis	6-8
	Cinygmula mimus	6-8		14-16	Cinygmula mimus	2-4	Ephemera simulans	16-18
	Paraleptophlebia debilis	4-6		10-12	Ephemerella inermis	2-4		14-16
				12-14	Paraleptophlebia debilis	6-8	Ephemerella inermis	2-4
				2-4	Ephemerella spinifera	8-10	Ephemera simulans	12-14
			Paraleptophlebia debilis	2-4				10-12
								8-10
GROUP 3	Cinygmula mimus	4-6	Ephemerella spinifera	8-10			Ephemerella inermis	4-6
Fluctuating								

Table 24. Relevant diatom taxa defining ingestion clusters of Stauffer 2 mayflies, see text for further explanation.

	30 July, 1975	18 October, 1975	14 February, 1976	23 April, 1976
GROUP 1	Cocconeis placentula *	Synedra sp. B *	Cocconeis placentula *	Achnanthes spp. *
Surface Feeders	Navicula cryptocephala +	Gomphonema sp. *	Nitzchia sp. A +	Navicula sp. B +
		Navicula sp. A +	Cymbella cymbiformis *	Cocconeis placentula *
		Cymbella sinuata *	Fragilaria leptostauron +	Fragilaria leptostauron var. dubia +
GROUP 2	Fragilaria construens +	Fragilaria construens +	Fragilaria construens +	Gyrosigma sp. +
Interstitial Feeders	Other species	Fragilaria leptostauron var. dubia +	Synedra sp. A *	Fragilaria construens +
	Fragilaria leptostauron var. dubia +	Fragilaria leptostauron +	Other species	Synedra amphicephala +
	Fragilaria leptostauron +	Navicula tripunctata +	Fragilaria pinnata	Fragilaria leptostauron +
GROUP 3	Nitzchia sp. B +	Fragilaria pinnata		Fragilaria pinnata
Fluctuating	Navicula cryptocephala +	Cymbella sp. C *		Other species
	Navicula viridula +	Navicula tripunctata +		Fragilaria leptostauron var. dubia +
	Achnanthes *	Synedra sp. A *		

* Epilithic species

\+ Epipelic species

Group 1 nymphs therefore have been classified as *surface feeders*. Group 2 ephemeropterans represent species that feed in areas with relatively higher epipelic diatom populations, namely interstices or the rock surfaces directly exposed to them, and I call these *interstitial feeders*. Members of Group 3 do not fit either category; these nymphs may feed in either area and are referred to as *variable* in feeding habits.

Analysis of Stauffer 1 mayflies belonging to each group indicates that all size classes of *Cinygmula mimus*, on all dates analyzed, are surface feeders. Conversely, *Ephemerella inermis* and *E. tibialis* nymphs are consistent interstitial feeders. *Baetis* spp. size classes fluctuate between the two groups. *Ephemerella spinifera* always clustered separately as a third group, as did the 2-4 mm class of *Baetis* nymphs on 14 February 1976.

The diatom associations at Stauffer 2 were similar to those of Stauffer 1 except for more frequent occurrence of epipelic diatom species in nymphs of the Group 1 clusters (Tables 23, 24). This may be due to the greater diatom diversity at Stauffer 2 or to a slower current velocity and greater mean depth allowing more frequent occurrence of epipelic diatoms in surface habitats at this site. In contrast to Stauffer 1, *Baetis* spp. were consistent members of the surface feeding group at Stauffer 2. They were the only

Table 25. PC analysis summary of ingested diatoms for various size classes of nymphs, Tay River.

	10 July, 1975		14 November, 1975		14 February, 1976		13 May, 1976	
GROUP 1	Cinygmula mimus	4-5	Cinygmula mimus	2-4	Cinygmula mimus	6-8	Baetis persecuta	4-6
Surface Feeders		3-4		4-6		2-4		2-4
		6-7		6-8	Baetis persecuta	2-4	Cinygmula mimus	4-6
	Epeorus sp.	5-6			Rhithrogena sp.	6-8		6-8
		7-8			Ephemerella inermis	2-4		2-4
		6-7			Cinygmula mimus	4-6	Ephemerella flavilinea	2-4
	Baetis persecuta	6-8			Ameletus sparsatus	4-6	Epeorus sp.	2-4
		2-4			Paraleptophlebia sp.	4-6		
	Ephemerella flavilinea	8-9						
	Baetis persecuta	4-6						
	Ephemerella inermis	6-8						
	Cinygmula mimus	7-8						
	Ephemerella inermis	4-5						
	Cinygmula mimus	5-6						
	Ephemerella tibialis	2-3						
	Paraleptophlebia sp.	2-4						
GROUP 2	Pseudocloeon sp.	2-4	Rhithrogena sp.	4-6	Paraleptophlebia sp.	6-8	Paraleptophlebia sp.	4-6
Interstitial Feeders		4-6	Ephemerella spinifera	8-10	Ameletus sparsatus	10-12		6-8
	Ephemerella flavilinea	6-8	Baetis persecuta	2-4		12-14		
	Ephemerella tibialis	4-6	Paraleptophlebia sp.	4-6		8-10		
			Rhithrogena sp.	6-8		6-8		
			Ephemerella spinifera	6-8	Paraleptophlebia sp.	2-4		
			Ameletus sparsatus	8-10				
GROUP 3			Paraleptophlebia sp.	2-4	Paraleptophlebia sp.	2-4		
Fluctuating				4-6				

Table 26. Relevant diatom taxa defining ingestion clusters of Tay River mayflies, see text for further explanation.

	10 July, 1975	14 November, 1975	14 February, 1976	13 May, 1976
GROUP 1	Cymbella sinuata *	Cymbella spp. *	Cymbella sinuata *	Gomphonema sp. A *
Surface Feeders	Gomphonema sp. A *	Cocconeis placentula *	Other species	Cocconeis placentula *
	Cocconeis placentula *	Cymbella sinuata *	Navicula sp. A +	Cymbella spp. *
	Achnanthes spp. *	Achnanthes spp. *	Gomphonema sp. A *	Cymbella sinuata *
	Other species		Cymbella spp. *	Achnanthes spp. *
	Navicula sp. A +		Cocconeis placentula *	Other species
	Navicula tripunctata +			
GROUP 2	Navicula cryptocephala +	Cymbella spp. +	Achnanthes spp. *	Navicula sp. A +
Interstitial Feeders	Synedra amphicephala +	Diatoma sp. +	Cymbella spp. +	Achnanthes spp. *
	Didymosphenia geminata	Synedra amphicephala +	Navicula tripunctata +	Fragilaria construens +
	Cymbella spp. +	Navicula cryptocephala +	Didymosphenia geminata	Cymbella spp. +
	Navicula tripunctata +	Fragilaria construens +	Synedra sp. B *	Synedra amphicephala +
	Navicula sp. A +	Synedra sp. B *	Fragilaria construens +	Nitzchia sp. B +
	Synedra sp. B *	Nitzchia sp. B +	Meridion circulare *+	Other species
			Nitzchia sp. B +	Navicula cryptocephala +
				Navicula tripunctata +
GROUP 3		Navicula tripunctata +	Cocconeis placentula *	
Fluctuating		Navicula sp. A +	Other species	
		Other species		
		Cocconeis placentula *		

* Epilithic species; + Epipelic species.

species to occur entirely in this group. *Ephemerella inermis* nymphs were surface feeders during July and October, but interstitial feeders during February and April. *Leptophlebia* nymphs were primarily members of the surface group, except for the 2-4 mm nymphs on 14 February. *Paraleptophlebia debilis* size classes usually belonged to the interstitial group during summer and autumn, with a switch to the surface group by most size classes during spring and summer. *Ephemera simulans* nymphs were always interstitial feeders except for the 2-4 mm size class in April. *Cinygmula mimus* populations were consistently interstitial feeders, and this is in contrast to members of the Stauffer 1 population, which were surface feeders. *Ephemerella spinifera* nymphs occurred in all three groups.

Tay River surface feeders include all *Cinygmula mimus*, *Epeorus* sp., *E. inermis* and most *Baetis persecuta* nymphs (Tables 25, 26). The summer species *Ephemerella flavilinea* and *E. tibialis* had members in both groups, with a general trend for very small nymphs to be mainly surface feeders. Interstitial feeders in the Tay River included *E. spinifera* and *Pseudocloeon* sp. specimens of all samples analyzed. *Paraleptophlebia* specimens usually belonged to the interstitial group, however on two occasions the nymphs clustered out as surface feeders.

Table 27. PC analysis summary of ingested diatoms for various size classes of nymphs, Bigoray River.

	30 July, 1975		10 October, 1975		20 March, 1976		14 May, 1976	
GROUP 1	Stenacron canadense	8-10	Callibaetis coloradensis	2-4	Siphloplecton basale	14-15	Callibaetis coloradensis	4-6
Surface Feeders	Centroptilum sp.	2-4		4-6		13-14	Leptophlebia cupida	6-8
	Baetis tricaudatus	4-6		6-8		11-12	Callibaetis coloradensis	6-8
		2-4		8-10		16-17		
	Centroptilum sp.	6-8				15-16		10-12
	Paraleptophlebia debilis	6-8					Siphlonurus alternatus	2-4
	Centroptilum sp.	4-6					Leptophlebia cupida	12-14
		8-10					Callibaetis coloradensis	8-10
	Paraleptophlebia debilis	4-6					Siphloplecton basale	16-18
							Leptophlebia cupida	10-12
							Siphloplecton basale	14-15
								13-14
GROUP 2	Siphlonurus alternatus	10-12	Ephemera simulans	14-16	Leptophlebia cupida	6-7	Leptophlebia cupida	8-10
Interstitial Feeders		8-10	Leptophlebia cupida	6-8		10-12		5-6
				2-4		7-8	Ephemera simulans	20-22
	Callibaetis coloradensis	4-6	Siphlonurus alternatus	8-10		5-6	Caenis simulans	4-6
			Ephemera simulans	2-4		3-4	Ephemera simulans	2-4
						8-9		4-6
			Siphlonurus alternatus	10-12		9-10		
			Leptophlebia cupida	4-6				

Table 28. Relevant diatom taxa defining ingestion clusters of Bigoray River mayflies, see text for further explanation.

	30 July, 1975	10 October, 1975	20 March, 1976	14 May, 1976
GROUP 1	Achnanthes spp. *	Epithemia sp. B *	Achnanthes spp. *	Synedra sp. A *
Surface Feeders	Cocconeis placentula *	Fragilaria sp. +	Diploneis sp. +	Other species
	Epithemia sp. B *	Cymbella sinuata +	Fragilaria leptostauron +	Nitzchia sp. C +
	Nitzchia sp. B +	Cyclotella sp. A. +	Cyclotella sp. A +	Cyclotella sp. B +
		Gomphonema sp. A *		Meridion circulare *+
		Epithemia A. *		
GROUP 2	Synedra sp. A *	Gyrosigma sp. +	Nitzchia sp. A +	Diploneis sp. +
Interstitial Feeders	Nitzchia sp. C +	Nitzchia sp. B +	Other species	Epithemia sp. C *
	Other species	Achnanthes spp. *	Synedra sp. A +*	Surirella sp. +
	Navicula cryptocephala +	Navicula cryptocephala +	Cocconeis placentula *	Stauroneis sp. +
	Fragilaria leptostauron +		Navicula sp. A +	Cymbella sp. C +
	Navicula pupula +		Nitzchia sp. C +	Nitzchia sp. A +
	Navicula tripunctata +		Epithemia sp. C *	

* Epilithic species

\+ Epipelic species

Interpretation of cluster analyses of consumed diatoms is more complicated for the Bigoray River mayflies because sampling was not restricted to a riffle area. I also sampled amongst the emergent shoreline vegetation and in slow water areas. Cluster and PCA, as at the other sites, nevertheless resulted in two main groups, with predominantly epilithic diatoms in Group 1 guts and epipelic diatoms in Group 2 guts (Tables 27, 28). However, the possibility of ingestion of epiphytic diatoms must also be considered for the Bigoray River mayflies. It is sometimes difficult to differentiate between epilithic and epiphytic diatom species because the same species often inhabit both substrate types (Round 1964, Hutchinson 1975). Some of the diatom species from Bigoray River gut samples, classified as epilithic, may have been derived from epiphytic habitats. Surface feeders from the Bigoray River therefore include grazers on rock surfaces and also aquatic macrophytes. Bigoray River surface feeders included *Baetis tricaudatus*, *Centroptilum* sp., *Paraleptophlebia debilis*, *Siphloplecton basale* and *Stenacron interpunctatum*. *Callibaetis coloradensis* nymphs were also in Group 1 except for the 4-6 mm nymphs of the 30 July 1975 sample. The *Caenis simulans* and *Ephemera simulans* populations were entirely in Group 2. *Leptophlebia cupida* and *Siphlonurus alternatus* specimens

were also interstitial feeders except for certain very large *L. cupida* and small *S. alternatus* nymphs.

DISCUSSION

General

Detritus was the major food item consumed by all ephemeropteran taxa studied, with diatoms second in importance. Filamentous algae, sand grains and animal material were usually detected in only trace quantities.

Several workers (Jones 1950, Chapman and Demory 1963, Egglishaw 1964, Mundie 1974, Moore 1977, Gray and Ward (in press)) have indicated the importance of detritus to primary consumers in streams. The general reliance on detritus by a significant portion of stream invertebrates may reflect adaptation to the most reliable food resource. Detrital material is available in streams throughout the year, whereas green plant material fluctuates greatly in response to numerous factors (Jones 1950).

The relative nutritive values of detritus and living plant material (principally diatoms) has not been clearly defined. Some researchers (Brown 1960, Hargrave 1970, Kofoed 1975), relying on growth rate studies, imply that algae are of greater nutritive value than detritus. Calorific values indicate that detritus and algae may be similar (detritus slightly higher) in respect to calories per gram (Trama 1972, Cummins 1973). However, relative energy values

expressed per unit dry weight may be misleading when comparing relative volumes of ingested material.

I determined the dry weight to volume ratio of detritus for Salix sp. leaves from a local stream. The leaves were dried, ground in a mill, and resuspended in distilled water. Using the Coulter Counter, I determined detrital volume estimates, which were then compared to dry weight determinations of similar size subsamples. Results indicated a value of 1.322 mg/mm^3 for leaf material. Trama (1967) reported a ratio of 2.182 mg/mm^3 for diatoms. If calories per unit weight are similar for diatoms and detritus, the above values indicate that per unit volume diatoms have the potential of being a more concentrated food resource. This argument is further enhanced by findings that the major assimilative component of detritus is probably its associated microflora of bacteria and fungi (Hargrave 1970, Kofoed 1975). Calories contained in the detrital material per se may be mostly unavailable. Detritus can be considered a substrate that the consumer must pass through its gut to obtain the nutritionally important microflora that colonizes it.

Based on volumes consumed, most species of my study undoubtedly received most of their nutrition from detritus. Indeed, for many species, diatoms composed less than 5% of the ingested volume throughout the life cycle. For species exhibiting relatively high diatom consumption (at times 25% or greater), diatoms

likely provided a significant if not the largest, portion of the assimilated energy during these periods.

Lotic autotrophs (especially diatoms and green algae) may serve as a high energy food resource that is available on a seasonal basis. In many instances detritus may be the base food resource, with diatoms providing additional energy necessary during critical periods, e.g. rapid growth phases and during certain developmental stages.

Lack of significant filamentous algae ingestion by mayfly nymphs has been noted in other studies (Brown 1961, Moore 1975, Gray and Ward 1978). Filamentous algae were occasionally very abundant in my streams but there was never a corresponding increase in the ingestion of these algae. Possibly, the nymphs may have difficulty in consuming the large filaments or in digesting the cell walls. Gray and Ward (in press) postulate that these algae may be avoided because of their low energy content.

Sand grains were consumed only in trace quantities, and this may reflect efficient presorting of consumed particles. Selection against mineral particles is reasonable from a nutritive aspect, however Brown (1961) maintains that the adhering microflora of consumed sand grains could provide some nutrition.

Food Habit Regimes

Most workers have concluded that aquatic insect food habits are dependent upon the type and amount of all material available, termed polyphagy (Brown 1961, Agnew 1962, Chapman and Demory 1963, Minckley 1963, Calow 1970, Koslucher and Minshall 1973, Hall and Pritchard 1975, Gray and Ward (in press). In contrast, monophagy is the selection of one or a few food resources from the broad spectrum of available ones. Although food habits of most aquatic insects do appear to be mainly influenced by food availability, differences in both types and relative quantities of materials consumed at a particular site do occur. Within the framework of polyphagy these differences can be accounted for by microhabitat partitioning amongst the nymphs. If a population of immature aquatic insects or a particular size class within the population commonly feed in a particular microhabitat, the material consumed will reflect the type of food resources unique to that microhabitat. The material ingested will in turn be different from that consumed by other nymphs of other microhabitats.

By relating the diatom species ingested by each mayfly size class to the known microhabitat preference of the diatoms, I could broadly define the microhabitat in which each mayfly size class was feeding. Based

FOOD HABIT REGIMES

1. "SURFACE FEEDERS"
(Consume mostly epilithic diatoms)

↓

Proportionally high total diatom ingestion
(Epilithic standing crop dependent)

↓

Consume high proportion of small particles
(PSCI)

Average or Below Total Volume Consumed:

- Baetis spp. (Stauf 1)
- (Stauf 2)
- Baetis persecuta
- Baetis tricaudatus
- Callibaetis coloradensis
- Centroptilum spp.
- Ephemerella inermis (Stauf 2-Fall) (Tay)
- Cinygmula mimus
- Leptophlebia sp.
- Epeorus sp.

Average or Above Total Volume Consumed:

- Stenacron canadense
- Rhithrogena sp.
- Paraleptophlebia debilis (Bigoray)

2. "INTERSTITIAL FEEDERS"
(Consume mostly epipelic diatoms)

↓

Proportionally low total diatom ingestion

↓

Extension of range of particle size consumption to include a greater proportion of large particles (PSC II, III, IV)

Average or Below Total Volume Consumed:

- Baetis spp. (Stauf 1)
- Pseudocloeon sp.
- Caenis simulans
- Ephemerella flavilinea
- Ephemera simulans
- Ameletus sparsatus

Average or Above Total Volume Consumed:

- Ephemerella inermis (Stauf 1) (Stauf 2-Spring)
- Ephemerella tibialis
- Leptophlebia cupida
- Paraleptophlebia debilis (Stauf 2) *
- Siphloplecton basale **
- Siphlonurus alternatus

3. "VARIABLE FEEDERS"
(Diverse consumption of epipelic & epilithic diatoms)

↓

Variable total diatom ingestion

↓

Size of particles consumed variable

↓

Variable Total Volume

- Ephemerella spinifera
- Paraleptophlebia sp. (Tay)

* Particle sizes do not fit   ** Fits except for type of diatoms.

Figure 47. Food habits classification of all mayfly species studied. See text for further explanation.

on microhabitat preferences of diatoms, and also the other gut analysis parameters, e.g. total consumed volume, relative ingestion of diatoms, particle size, I established three "food habit regimes" into which each mayfly species was placed (Fig. 47).

The surface feeding group (1) contains populations that consume predominantly "epilithic diatoms" and therefore feed in a microhabitat where epilithic diatoms were most abundant, namely riffle substrates exposed to the current (i.e. surfaces and upper sides of rocks). This group also includes possible epiphytic grazers found in the Bigoray River.

The interstitial feeding group (2) contains populations that mainly consume epipelic diatoms. Included in this group would be mayflies that feed in areas where reduced current allows establishment of epipelic communities, e.g. dead water spaces between rocks, lower surfaces of the rocks themselves, and all the fine-grained depositional substrates that are common in pools and along stream margins.

The third category (3), "variable feeders", contains populations whose food habits included characteristics of both the above categories, e.g. populations ingesting relatively large quantities of both epipelic and epilithic diatoms. Category 3 does not include populations with some size classes

fitting group 1 and others fitting into group 2. These populations were placed in the category to which most of the gut samples belonged.

The first two groups are similar to the three microhabits Coffman (1967) defined for rocky stream beds. His first microhabitat included the surface of stones, which is similar to my surface feeding habitat. Interstitial feeders of my classification would encompass both Coffman's dwellers of open interstitial spaces and dwellers of sediment-filled interstitial spaces.

Quantity of diatoms consumed is another parameter I used to define the food habit regimes. Surface feeders tend to have a higher and more fluctuating diatom consumption rate when compared to the relatively stable and lower diatom consumption of the interstitial feeders. Diatoms are more abundant on exposed surfaces compared to interstices (Badcock 1949); therefore one would expect surface feeders to consume them in greater proportions. Fluctuations in group 1's diatom consumption reflect the seasonality of the epilithic standing crops. The great dependence on detritus by interstitial feeders reflects a low diatom standing crop and a high detrital accumulation in interstitial and depositional habitats. Group 3 members fluctuated greatly in their consumption of diatoms.

Particles ingested by mayfly nymphs ranged in size from 1.6-161 um. For the entire study, on average 65.4% of the food items consumed consisted of particles in PSCI (32 um or less). Less than 5% of the average volume ingested was greater than 100 um. The general ingestion of small particles (less than 1000 um) would place all the ephemeropterans studied in the small-particle collector category of Cummins (1973).

Size of particles within the guts varied with the food regimes. Surface feeders consumed a greater proportion of small PSCI particles (32 um or less), whereas interstitial feeders ingested greater proportions of PSCIII and IV particles. This again can be related to the different microhabitats of the nymphs: exposed surfaces of rocks tend to trap small detrital particles in the rocks boundary layer and bacterial coating, whereas larger detrital particles settle out in the interstices. Most diatoms are included in PSCI and II, however epilithic diatoms are often smaller than epipelic diatoms. The ingestion of predominantly small particles by surface feeders is due to a greater availability of diatoms and small detrital particles. Interstitial feeders ingest proportionally more large particles because particle sizes consumed include larger detrital particles present in depositional and interstitial habitats.

The total volume of material consumed varied more between food habit regimes than did the other parameters. Most surface feeders tended to ingest below average total volumes of material, whereas interstitial feeders, depending on the population, might consume either above or below average total volumes.

Below average total ingestion for a surface feeder and above average consumption for an interstitial feeder can possibly be explained in terms of energetics. If both species have similar gut clearing times, the interstitial feeder must process a greater quantity of material than the surface feeder to obtain a similar number of calories. This is because material ingested by the surface feeder, on average, has a higher nutritive value due to a greater diatom component. The interstitial feeder also ingests proportionally more large detrital particles, which also decreases the relative nutritional value of the food. A specific volume of large detrital particles has a smaller total surface area than an equal volume of small particles; therefore the total colonizing microflora would be higher per unit volume of small particles, and this would make these small particles a more concentrated food resource. A relatively larger gut volume among detritivores has previously been noted for aquatic insects (Jones 1950) and also snails (Calow 1975a).

Interstitial feeders found to ingest below average total volumes may have a more efficient detrital assimilation rate and faster gut clearing time (Calow 1975b, Moore 1975).

Inclusion of a population in one of the three food habit regimes means that most specimens investigated fit into that particular category. However, shifts from one food habit category to another, either by season or by size class, occurred quite often and will be discussed below.

Surface Feeders

The surface feeding regime was dominated by members of the Baetidae and Heptageniidae. Baetids have frequently been observed to prefer exposed surface habitats in relatively fast water (Gilpin and Brusven 1970, Edmunds et.al. 1976, Corkum et.al. 1977).

Stomach analyses from all sites and dates for *Callibaetis coloradensis*, *Centroptilum* spp. and *Epeorus* sp. fit the surface feeding category. Nymphs of *Epeorus* sp. are morphologically adapted to very fast water, and hence one would expect them to be feeding in this microhabitat. *Centroptilum* sp. nymphs from Stauffer 2 were not included in a PC analysis; however, for all other parameters, they fit the surface feeding category. *Callibaetis* nymphs have been reported

on and amongst aquatic macrophytes (Trost and Berner 1963), and this association was frequently observed at the Bigoray River. Callibaetids may therefore be epiphytic rather than epilithic feeders. *Leptophlebia* nymphs from Stauffer 2 were also surface feeders. An Arctic population of *Leptophlebia* has also been classified as surface feeding (Moore 1977).

Other ephemeropterans placed in the surface feeding category were more flexible in their feeding habits. *Baetis tricaudatus* and *Baetis* spp. populations from Stauffer 2 and *B. persecuta* (except for the 2-4 mm size class) from Tay River were surface feeders. However, the *Baetis* populations of Stauffer 1 fluctuated between surface and interstitial feeding patterns.

Ephemerella inermis populations from Tay River and Stauffer 2 were mainly surface feeders, whereas nymphs of this species from Stauffer 1 were interstitial feeders throughout the year. *Cinygmula mimus* populations were surface feeders throughout the year at Stauffer 1 and Tay River, but at Stauffer 2 the nymphs fluctuated between surface and interstitial feeders.

The populations with the most flexible food habits are often the ones that are abundant at various locations, e.g. *Baetis* spp., *E. inermis*, and *C. mimus*. Ability to readily change food habit regimes in

response to different environmental conditions may account for these species being found in a variety of habitats.

Interstitial Feeders

Members placed in this category include most ephemeropterans considered crawlers and burrowers (Bengtsson 1924), which often inhabit interstitial or depositional habitats (Edmunds et.al. 1976). The major families with representatives in this food habit regime are Ephemerellidae, Caenidae, Ephemeridae, and Siphlonuridae.

Ephemerella tibialis and *E. flavilinea* populations appear to be almost exclusively interstitial feeders. Similarly, *Ameletus sparsatus* and *Pseudocloeon* sp. populations from Tay River were interstitial feeders throughout all nymphal stages.

Two mayflies often cited as preferring interstitial or deposition habitats are *Ephemera simulans* and *Caenis simulans* nymphs, and in my study they ingested very high proportions of detritus at a uniform rate throughout the study. PC analysis consistently classified nymphs of both species as interstitial feeders. Rather surprisingly, total volume of material ingested for nymphs of both species was below the study average for all size classes. A

method of compensating for the relatively low quality material they were ingesting could be by decreasing the gut-clearing time. The *E. simulans* population was the only mayfly exhibiting a two year life cycle, and the relatively low quality food the nymphs consumed may be one factor accounting for this observation.

Bigoray River populations of *Siphlonurus alternatus* and *Leptophlebia cupida* were also interstitial feeders. The *Siphloplecton basale* population (Bigoray River) had similar food habits to *S. alternatus*; however, PC analysis of ingested diatoms would place *S. basale* nymphs in the surface category. This may be a function of a less definite partitioning of epipelic and epilithic diatoms in the slower moving Bigoray River, or the nymphs may actively feed in a number of habitats.

Variable Feeding Regime

The only populations placed in this category were those of *Ephemerella spinifera* and *Paraleptophlebia* sp. from Tay River. *Ephemerella spinifera* nymphs appeared to be facultative predators; however, large quantities of diatoms were also ingested. It is not difficult to visualize such a mayfly predator as being relatively far-ranging as it searches for food; therefore if diatoms were incidentally ingested, they could have been obtained from either interstitial or surface

habitats. The diatoms may also have been derived from prey digestive tracts; if so, they would reflect the habitat from which the prey was obtained.

Presence of *Paraleptophlebia* sp. nymphs in category 3 could be a function of their observed diurnal activity pattern (Chapman and Demory 1963, Gilpin and Brusven 1970, Corkum 1976), i.e. being interstitial during the day and surface dwelling at night.

Seasonal and Size Class Trends

Trophic habits of the species studied often varied with the season or during life cycle stages.

One seasonal occurrence was the fluctuation in the relative number of diatoms ingested, which corresponded to epilithic diatom standing crop oscillations. This was evident among populations with surface feeding regimes, e.g. *Baetis* spp., *Epeorus* sp., *Cinygmula mimus*, and *Ephemerella inermis*. Such seasonal patterns were not evident amongst the interstitial feeders.

Epilithic diatom population tended to peak most frequently during autumn months, and less frequently, after the ice goes out in spring. These peaks often coincided with optimal growth periods for many univoltine winter mayflies. Such life cycles usually include hatching during late August or early September and then rapid growth until ice-cover develops or water

temperatures become very low, usually in November. As water temperatures rise in spring, growth resumes with nymphs maturing during late spring or summer. Increased diatom consumption during these major spring and autumn growth periods may provide a "spike" of higher energy food which may be important for life cycle completion.

Ingestion of detritus by interstitial feeders was relatively uniform throughout the seasons; however, for surface feeders, peak detrital consumption most often occurred during late winter and early spring. At this time epilithic diatom populations are usually low (prior to the spring or early summer peak). In contrast, detritus in spring may be at its nutritional peak, having undergone mechanical and biological conditioning throughout the winter. By spring, the detritus would be broken into small enough particles for easy ingestion, and the essential microflora would have had time to colonize the particle, (Boling et.al. 1975). Examples of surface feeding mayflies exhibiting an early spring peak in detrital ingestion include Stauffer and Tay *Baetis* spp., *C. coloradensis*, *E. inermis*, and *C. mimus*. Gray and Ward (in press) also observed peak detrital ingestion during spring months in a Colorado stream.

Seasonal differences in the size of particles consumed occurred for both interstitial and surface

feeding mayflies. Interstitial feeders often consumed a greater proportion of large particles during autumn, e.g. *Baetis* spp. from Stauffer 1, *C. simulans* and *S. basale*. Autumn, when leaf input occurs, is the season when the proportion of large detrital particles in the stream is greatest. Therefore, an increase in the size of particles consumed by detrital feeders at this time would seem reasonable. Relatively smaller particles are consumed by interstitial nymphs after the ice goes out in spring; this, again reflecting mechanical and biological conditioning of detritus during winter. Surface feeding mayflies ingested relatively larger particles during spring than in the other seasons.

Stomachs from small nymphal size classes often contained above average proportions of small particles, examples include nymphs of *C. coloradensis*, *Centroptilum* sp., *E. inermis* from Stauffer Creek, *C. mimus*, *Leptophlebia* sp. and *S. alternatus*. It is difficult to ascertain if this is due to selection of small particles or simply a function of particle size availability.

Observations of elevated quantities of detritus from guts of small specimens (Coffman et.al. 1971, Cummins 1973) were also noted for some species of my study including some populations of *Baetis* spp. and *C. mimus*. When young nymphs first appeared in late

summer or early autumn, gut analysis frequently indicated an interstitial feeding regime with a corresponding high detrital ingestion rate. As the season progressed, diatom consumption often increased, coincident with a shift to surface feeding. Hatching most often takes place in the interstices; therefore an interstitial feeding regime amongst early instar nymphs seems reasonable (Coffman et.al. 1971).

Changes in feeding habits of mature nymphs were also noted. No food was ever found in the guts of nymphs that were in the last nymphal instar (characterized by dark wing pads). A reduced volume of ingested material by late instar nymphs was also frequently observed, e.g. *Rhithrogena* sp., *S. canadense*, *P. debilis*, and *L. cupida*. The lower ingestion rate likely reflects reduced availability of space in the body cavity due to development of adult structures, such as reproductive organs and wing pads. Some populations, notably *Baetis* spp. from Stauffer 1, *C. coloradensis*, *E. inermis*, *L. cupida*, although exhibiting a reduced total volume of food consumed, actually increased relative diatom ingestion during the late (but not last) nymphal instars. An increase in the quality of the food at this time partially compensates for the reduced quantity. Increased diatom consumption may also reflect selection of a surface microhabitat in preparation for emergence.

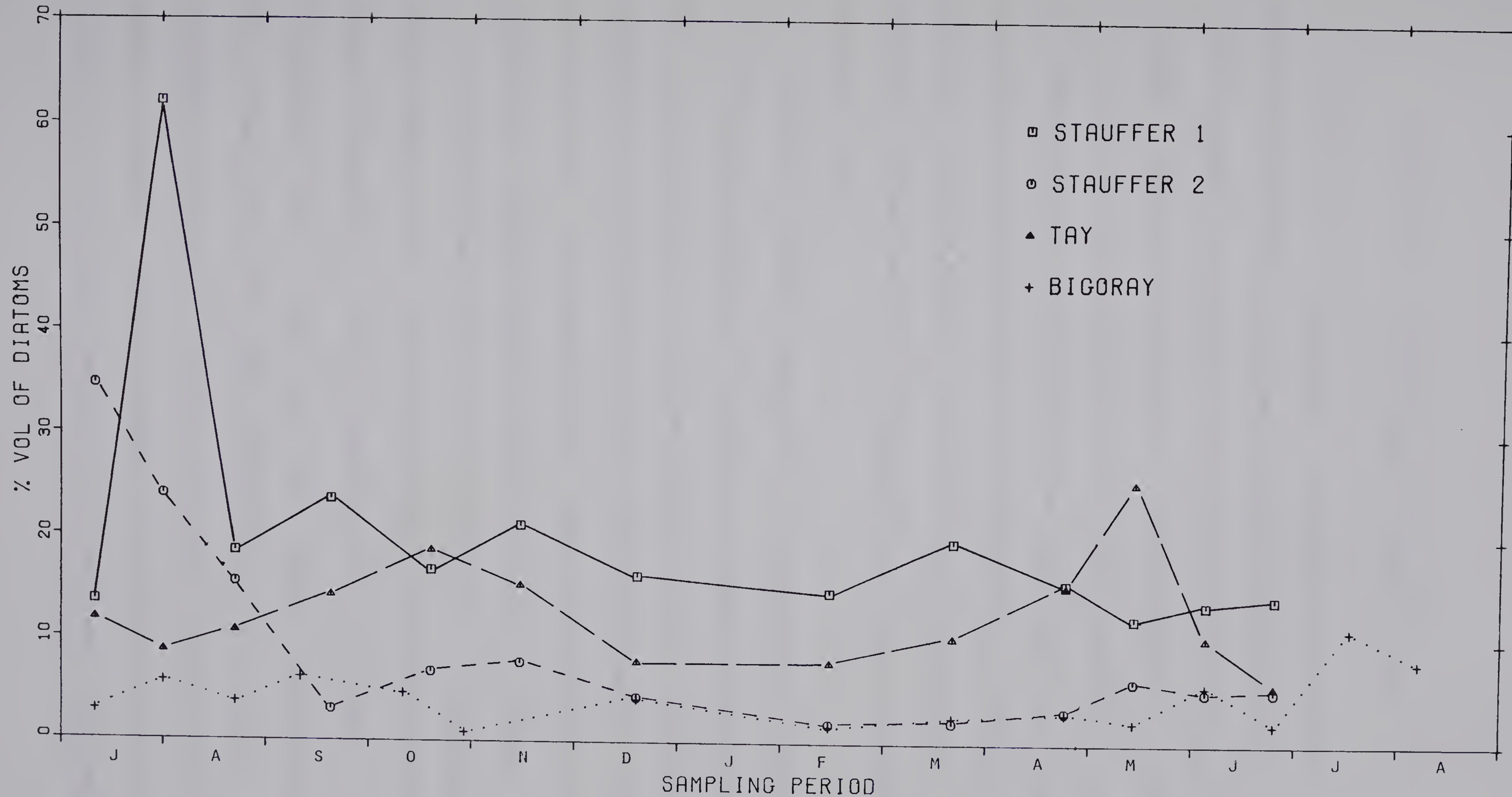

Figure 48. Seasonal trends in total consumption of diatoms by all species (1975-1976).

Food Habit Differences Between Sites

There were differences in mayfly food habit patterns between the three streams, particularly with respect to relative ingestion of detritus and diatoms. Total consumption of diatoms for all species, expressed as a proportion of the total material consumed for each date, are presented for all sites in Figure 48. Detrital ingestion can be considered the difference between percent diatom ingestion and 100 percent, since mineral matter and filamentous algae were relatively insignificant.

Overall diatom ingestion was highest at Stauffer 1, and intermediate at Tay River. Diatom consumption was consistently low in the Bigoray River, usually composing less than 5% of all ingested material. Mayflies of Stauffer 2 also exhibited a very low average diatom ingestion, except during summer and early autumn.

I postulated that diatoms would be a more important food component for the mayfly populations at Stauffer 1 than at Stauffer 2. This appears to be the case throughout much of the year, even though detritus was still the major food item ingested at both sites. Reliance on diatoms at both sites was greatest during summer. However, during autumn and winter, detritus completely dominated the material consumed (approximately

95%) at Stauffer 2; whereas at Stauffer 1, detrital ingestion was lower, near 80%. The different ingestion patterns between these two sites can largely be attributed to a greater abundance of interstitial feeders at Stauffer 2. Stauffer 1 was dominated by *Baetis* nymphs with *C. mimus* nymphs second in importance. Both species were predominantly surface feeders. The Stauffer 2 mayfly fauna was not dominated by *Baetis* spp.; there were a larger number of species present in more equitable numbers. Species of interstitial feeders that were not present at Stauffer 1, e.g. *P. debilis* and *E. simulans*, made up a large part of the Stauffer 2 mayfly fauna.

Based on the premise that ephemeropteran food habits are dependent upon available food resources, the observed differences between the two Stauffer Creek sites cannot be explained entirely by magnitude of the epilithic diatom densities. Diatom populations were generally higher at Stauffer 2, even though detrital ingestion was often greater at this site. Possibly relative abundance of detritus versus diatoms is more significant than absolute quantities. Stauffer 1, being close to the headwaters, receives little input of allochthonous material. Stauffer 2 has a greater portion of its flow derived from surface runoff, which, combined with extensive amounts of riparian vegetation

in the upstream reaches, would result in considerably more allochthonous organic input. More detritus at Stauffer 2 would indicate a more extensive food base of detritus as well as diatoms, which may in turn allow an expansion of species able to exploit it.

Of the four sites, the Bigoray River ephemeropterans were the most dependent upon detritus, and this is understandable when available food resources are analyzed. Epilithic diatom standing crops of the Bigoray River were low throughout much of the year, except for an early summer peak. The large autumn diatom populations observed at the other sites were not present in the Bigoray River. The stream supports mainly detrital-based mayflies such as L. cupida, S. basale, S. alternatus, C. simulans and S. canadense.

It is interesting to note that the surface feeders from Bigoray River were either summer species, i.e. P. debilis and Centroptilum spp. or winter species that exhibited peak growth phases during late spring and summer, when epilithic diatoms were abundant. The summer diatom peak may be a requisite for successful completion of these type life cycles. Lack of an autumn diatom peak could be one reason why few surface feeding species are found in the Bigoray River.

In respect to overall relative consumption of diatoms, the Tay River mayfly fauna was intermediate

to the Stauffer Creek and Bigoray River faunas. Tay River epilithic standing crops were large compared to the other sites, and one would also expect detrital input to be high because of the large forested watershed, much of which is composed of deciduous trees. The relatively high availability of both detritus and diatoms might be one reason why the Tay River exhibits a mayfly fauna consisting of large numbers of both surface and interstitial feeders.

Life Cycle Differences Between Sites

I found significant life history differences between *L. cupida* and *P. debilis* of the Bigoray River and these species in the other streams. Subimagoes of *Leptophlebia* sp. (presumably *L. cupida*) from Stauffer 2 emerged much earlier than *L. cupida* subimagoes from Bigoray River. The *P. debilis* populations from Stauffer Creek and Tay River had bivoltine life cycles, whereas *P. debilis* from Bigoray River had a univoltine summer life cycle. These differences may partially be due to food habit differences. *Leptophlebia* nymphs were surface feeders in Stauffer 2 with relatively high diatom ingestion. In contrast, *Leptophlebia* nymphs in the Bigoray River were interstitial feeders dependent upon detritus. Earlier emergence of *Leptophlebia* subimagoes in Stauffer Creek may be related

to more rapid spring growth (and development), due to ingestion of higher quality food at this time. *Paraleptophlebia debilis* nymphs are surface feeders in Bigoray River and they may rely on the summer diatom peak for completion of the life cycle. The absence of a winter generation in the Bigoray River may be partially related to the absence of large number of available diatoms in late summer and autumn.

SUMMARY

1. The Coulter Electronic Particle Counter proved to be a valuable tool in determining the size and total volume of materials ingested by mayfly nymphs. Most species were observed to ingest particles up to 160 um in diameter, with an average of 65% of all materials composed of particles less than 32 um in diameter.
2. Detritus was the dominant food item ingested, based on volume, with diatoms being second in importance. Mineral particles, filamentous algae and animal tissue were generally present in only trace amounts. Although diatoms rarely exceeded detritus in quantity consumed, they likely were nutritionally very important.
3. The hypothesis that material consumed is dependent upon relative availability appears to apply in my study. By relating the type of diatoms ingested to the known microhabitats of the diatoms, I could determine the microhabitat in which the ephemeropterans were feeding.
4. Using numerical classification techniques, I could define two major food habit regimes for the species studied. These regimes relate to the

microhabitat in which the mayfly was feeding. These regimes and their characteristics are:

I. Surface Feeders	II. Interstitial Feeders
a. Consume predominantly epilithic diatoms.	a. Consume predominantly epipelic diatoms.
b. High or fluctuating total diatom ingestion.	b. Low, uniform diatom ingestion.
c. Consume high proportions of small particles.	c. Consume greater proportion of large particles.
d. Most often ingest below average total volume of material.	d. Total volume ingested varied with the species.

5. Peak spring and autumn epilithic diatom populations coincided with high diatom ingestion by surface feeders and often correlated with elevated mayfly growth rates.
6. Detrital material was often most important as a food resource during late winter and spring.
7. Interstitial feeders seasonally ingested more large particles during autumn and surface feeders ingested more large particles in spring.
8. Very small nymphs of some populations were observed to ingest higher than average quantities of detritus and below average size particles. These observations may be due to microhabitat selection and food

availability rather than selectivity.

9. For all sites studied, detritus was ingested in greatest proportions throughout the year by the Bigoray River mayfly fauna. Diatoms were relatively most important as a food resource for ephemeropterans at the upstream Stauffer Creek Site. The mayfly populations at the downstream Stauffer Site generally relied more on detritus than at the upstream site, closer to the headwaters. Tay River had a very diverse ephemeropteran fauna of both interstitial and surface feeding species. This may be related to the large number of epilithic diatoms and high detrital content in this river.

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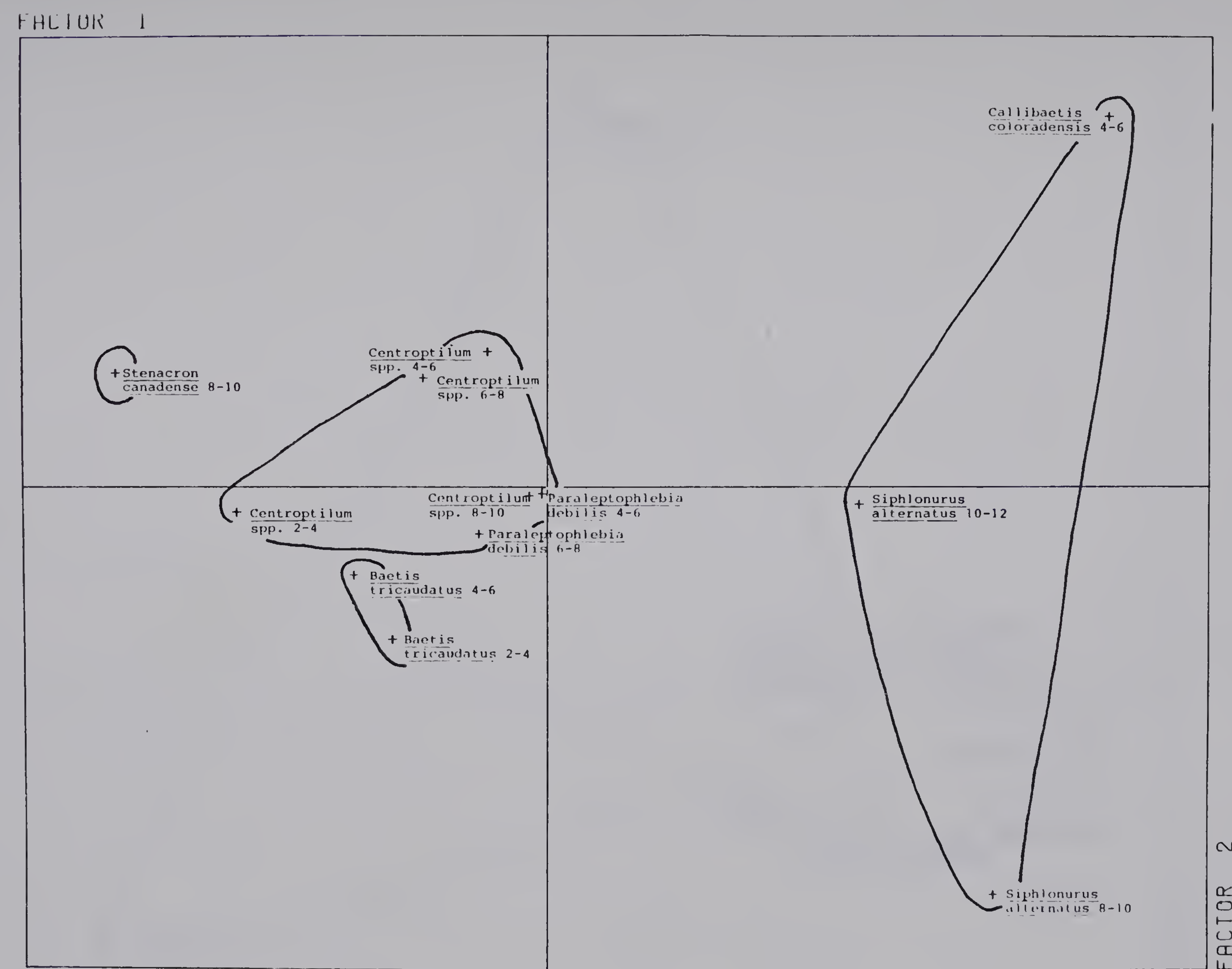
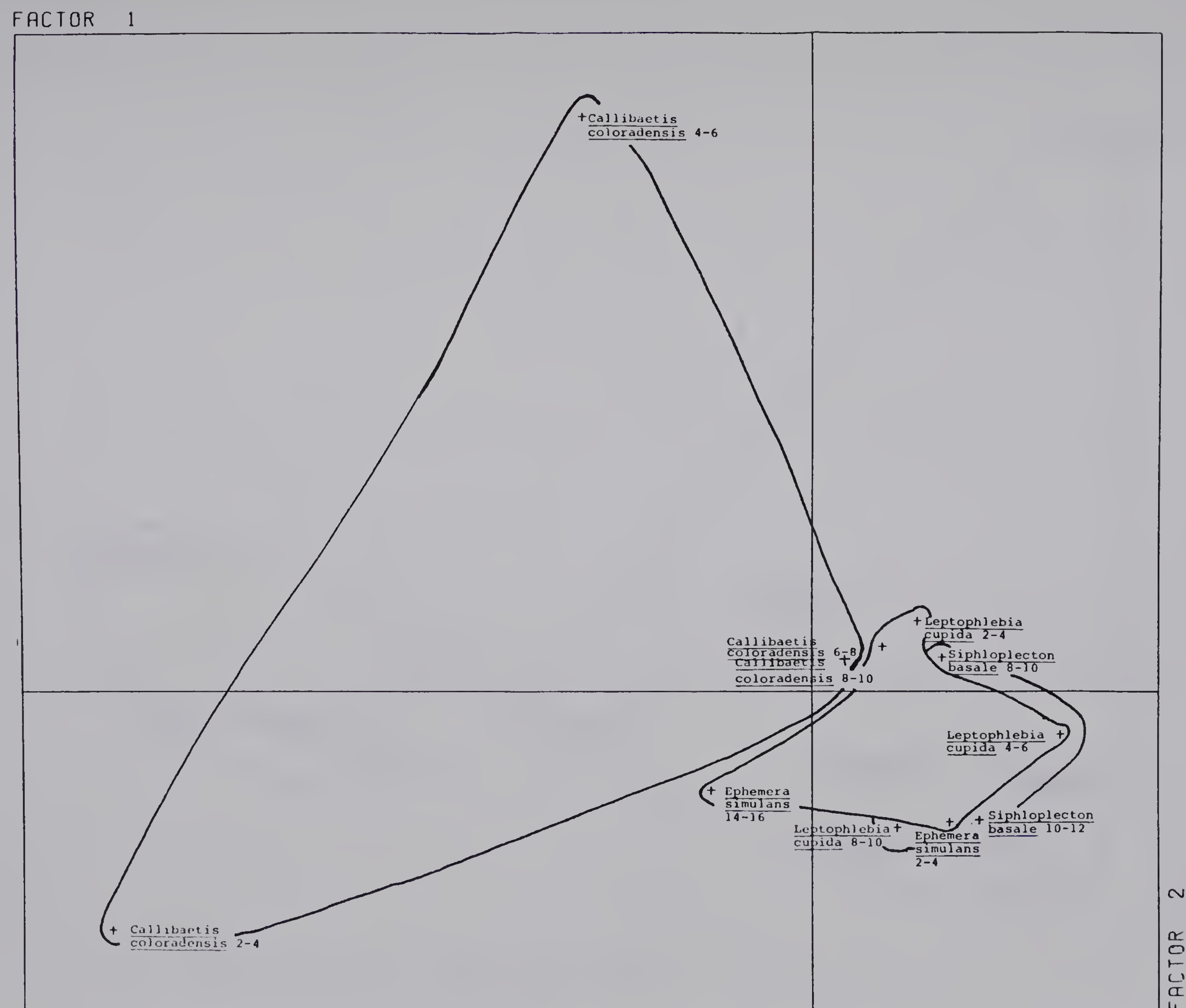
APPENDIX

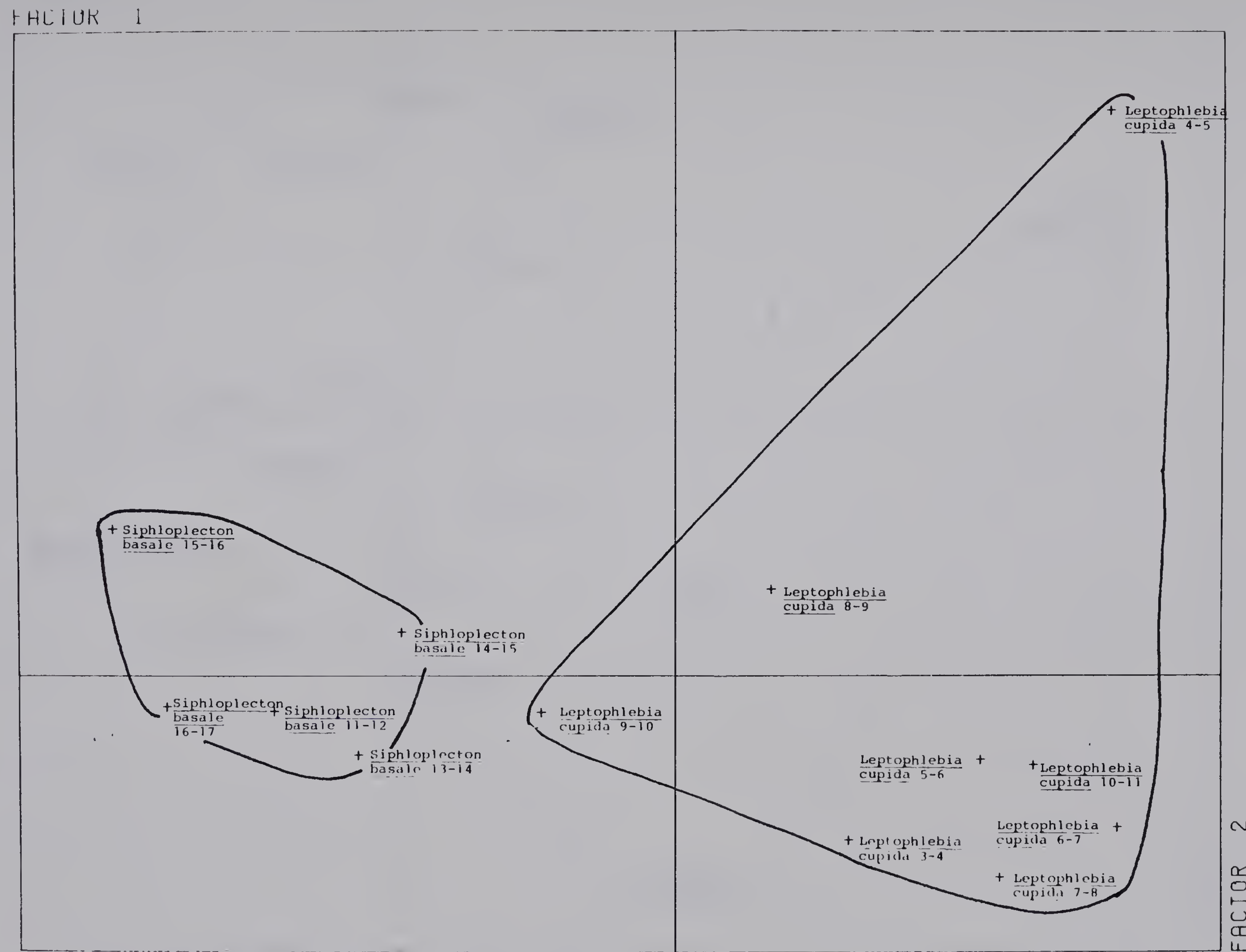
Factor scores for principal components 1 and 2 of stomachs analyzed for the various sites and dates.



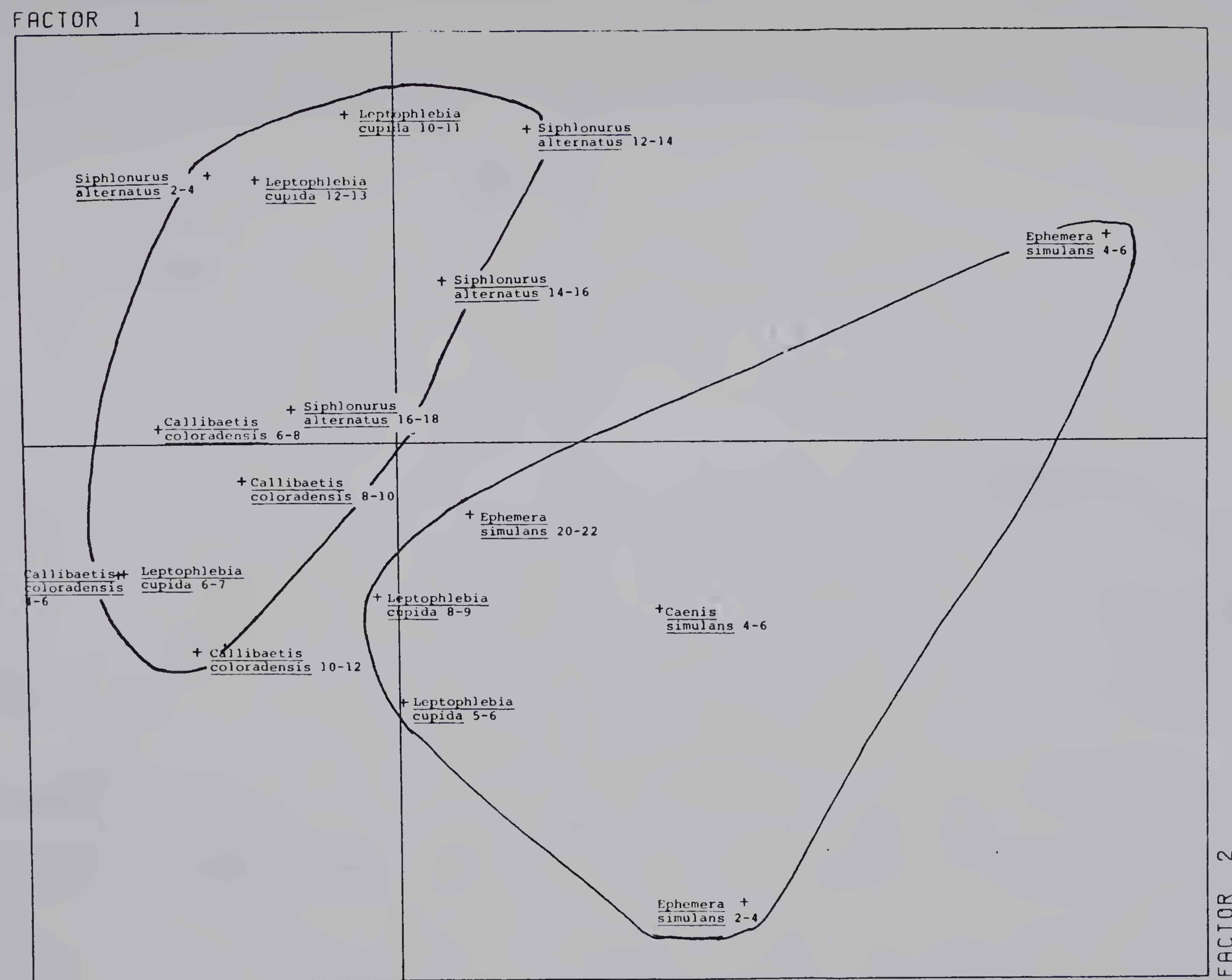
A. Bigoray River, 30 July 1975



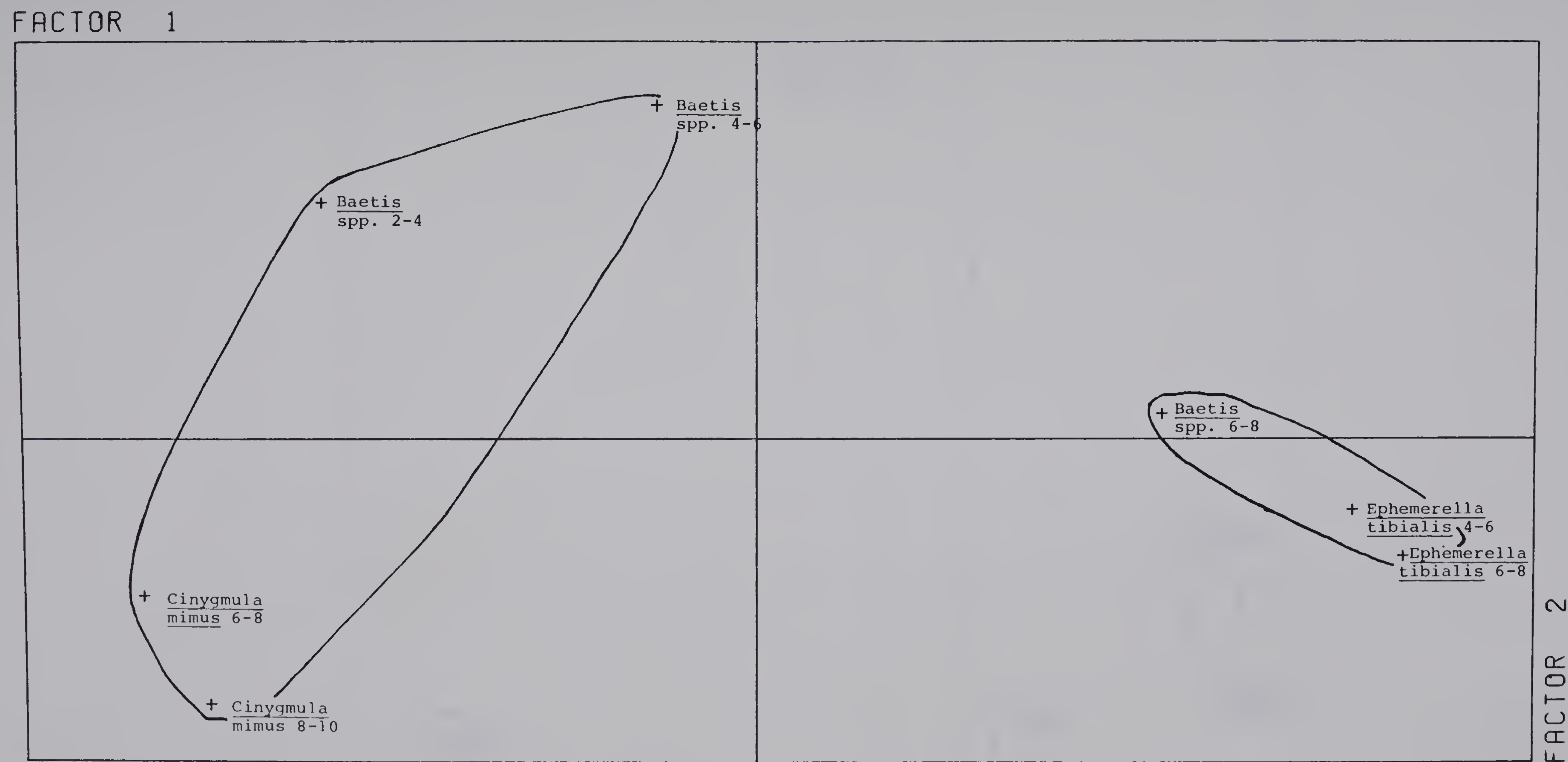
B. Bigoray River, 10 October 1975



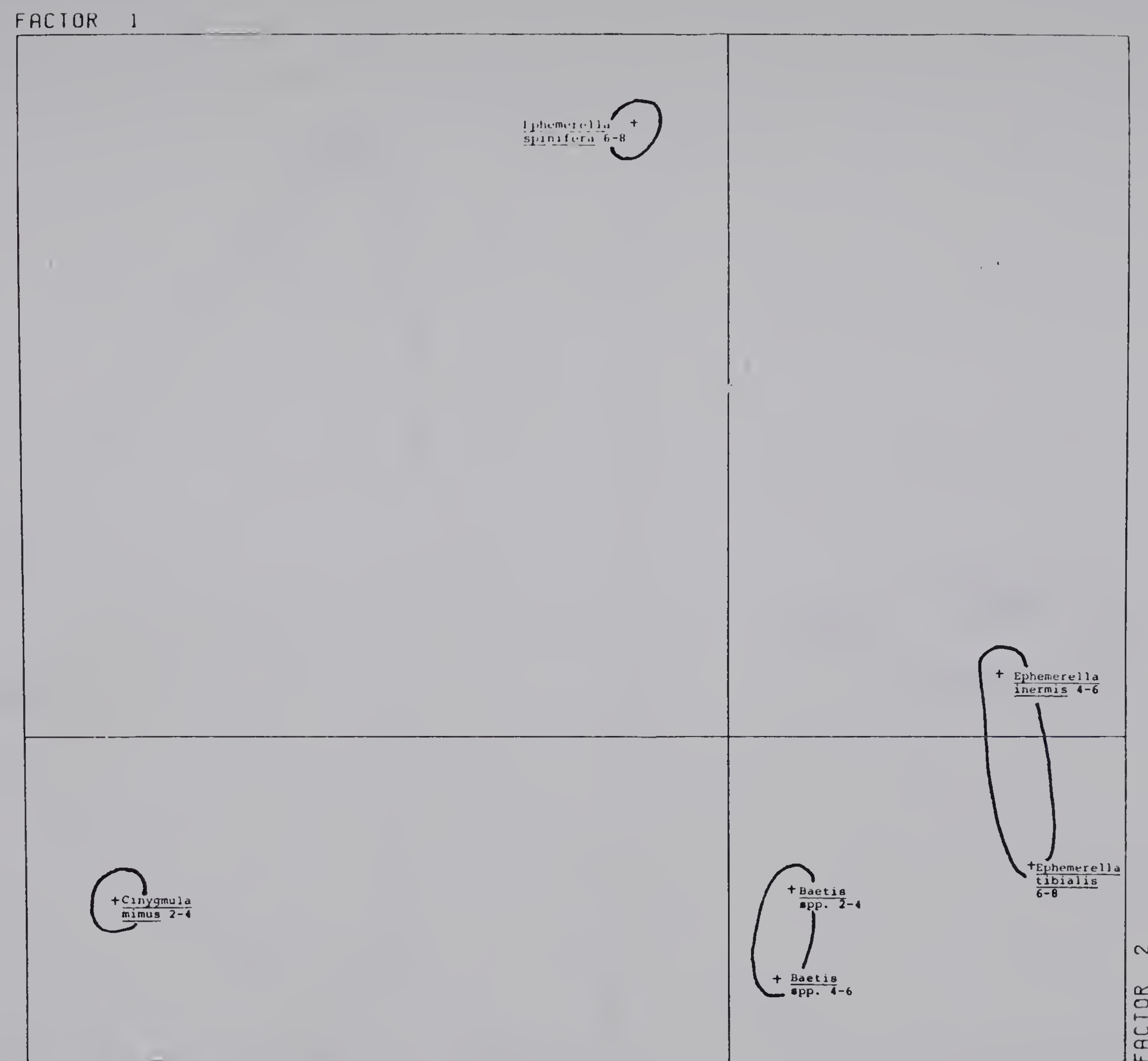
C. Bigoray River, 20 March 1976



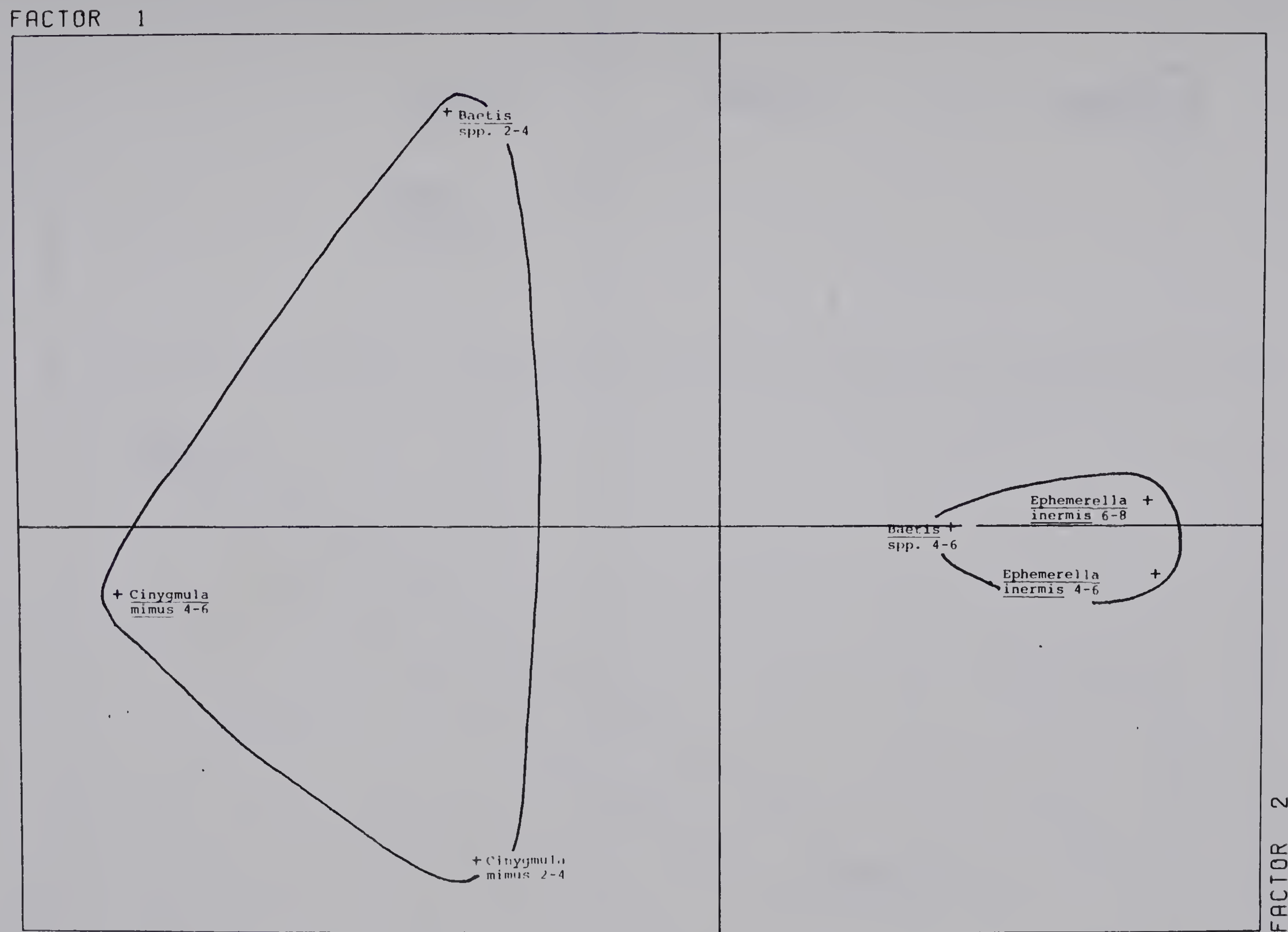
D. Bigoray River, 14 May 1976



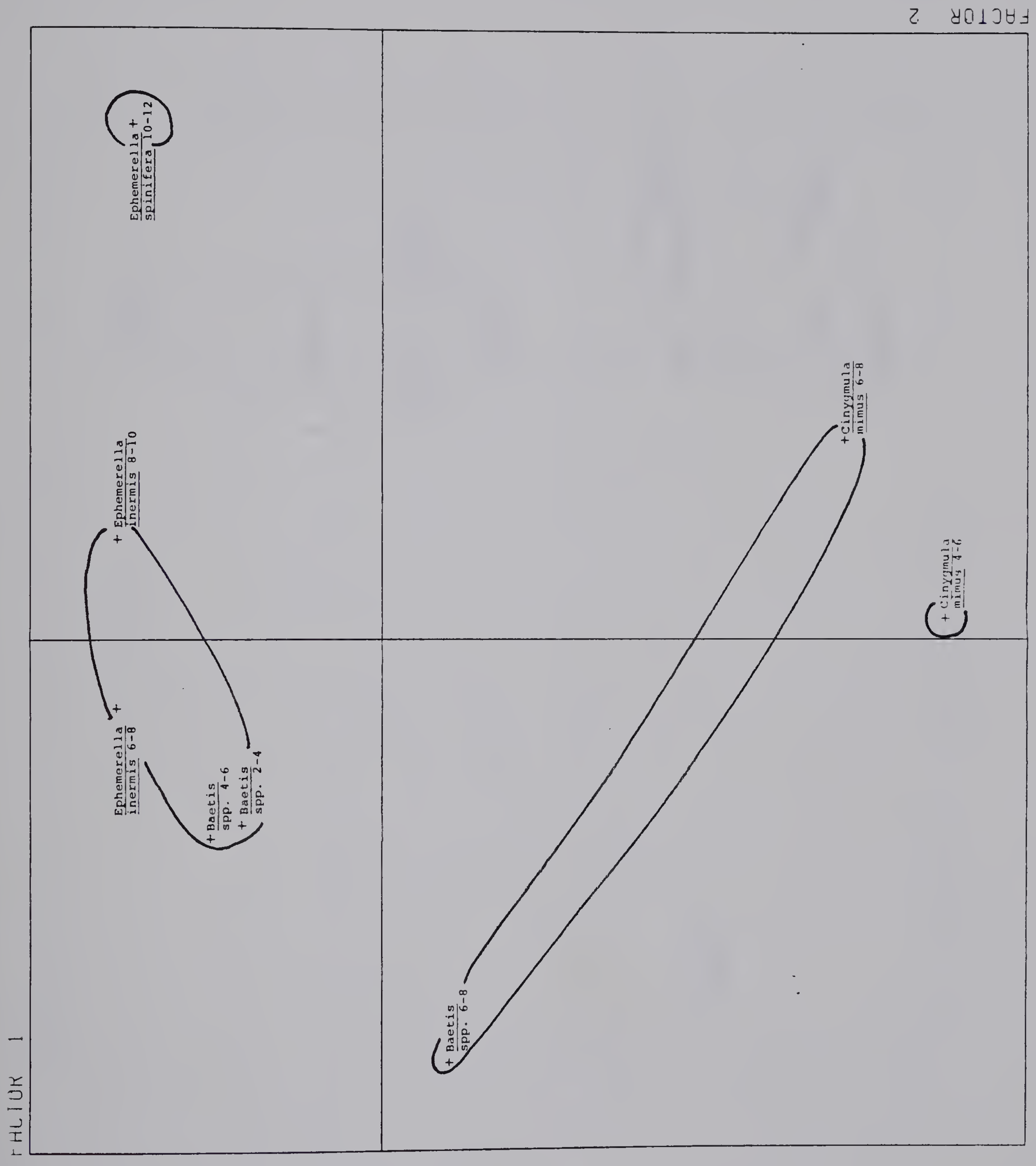
E. Stauffer 1, 30 July 1975



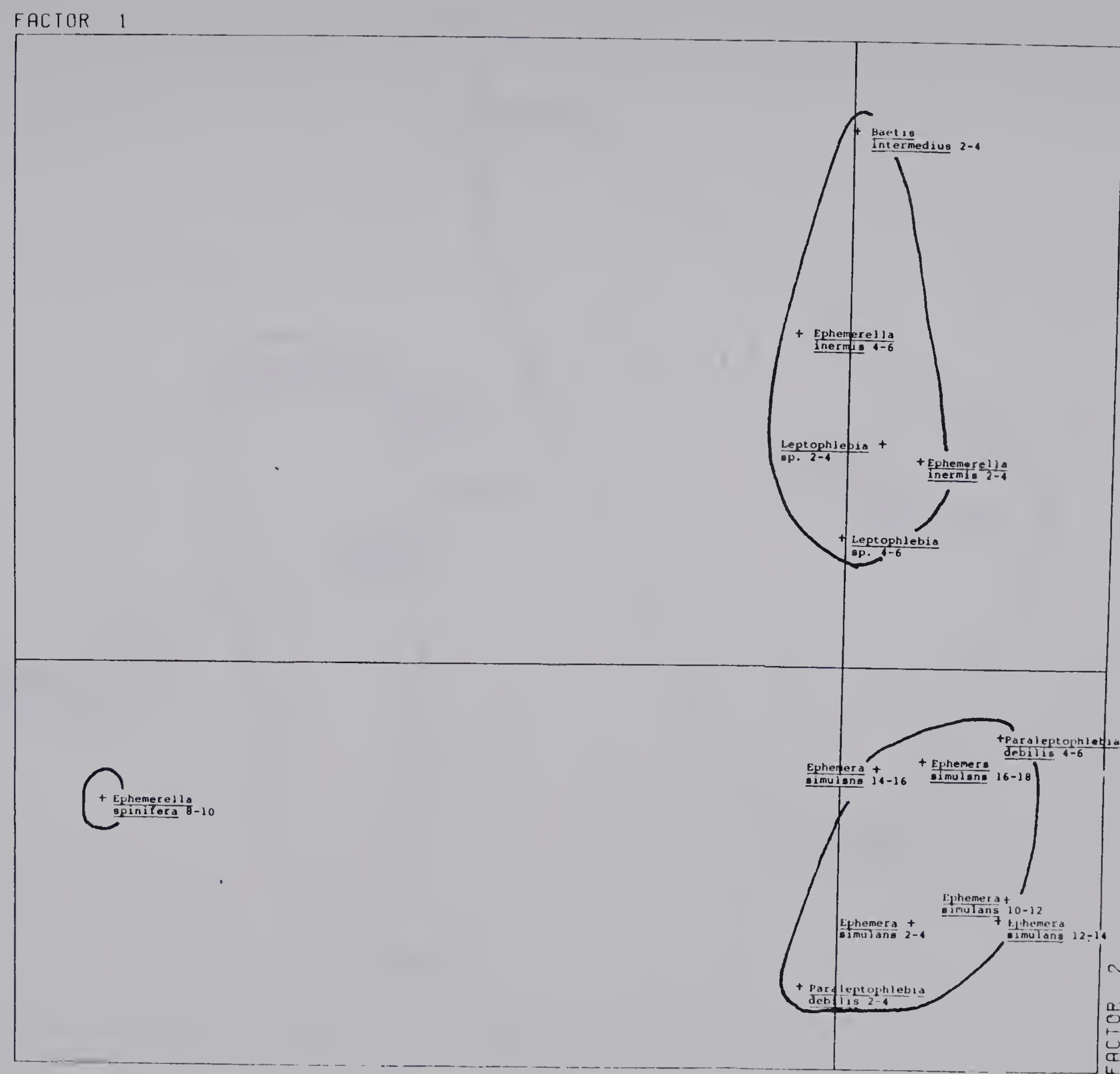
F. Stauffer 1, 14 November 1975



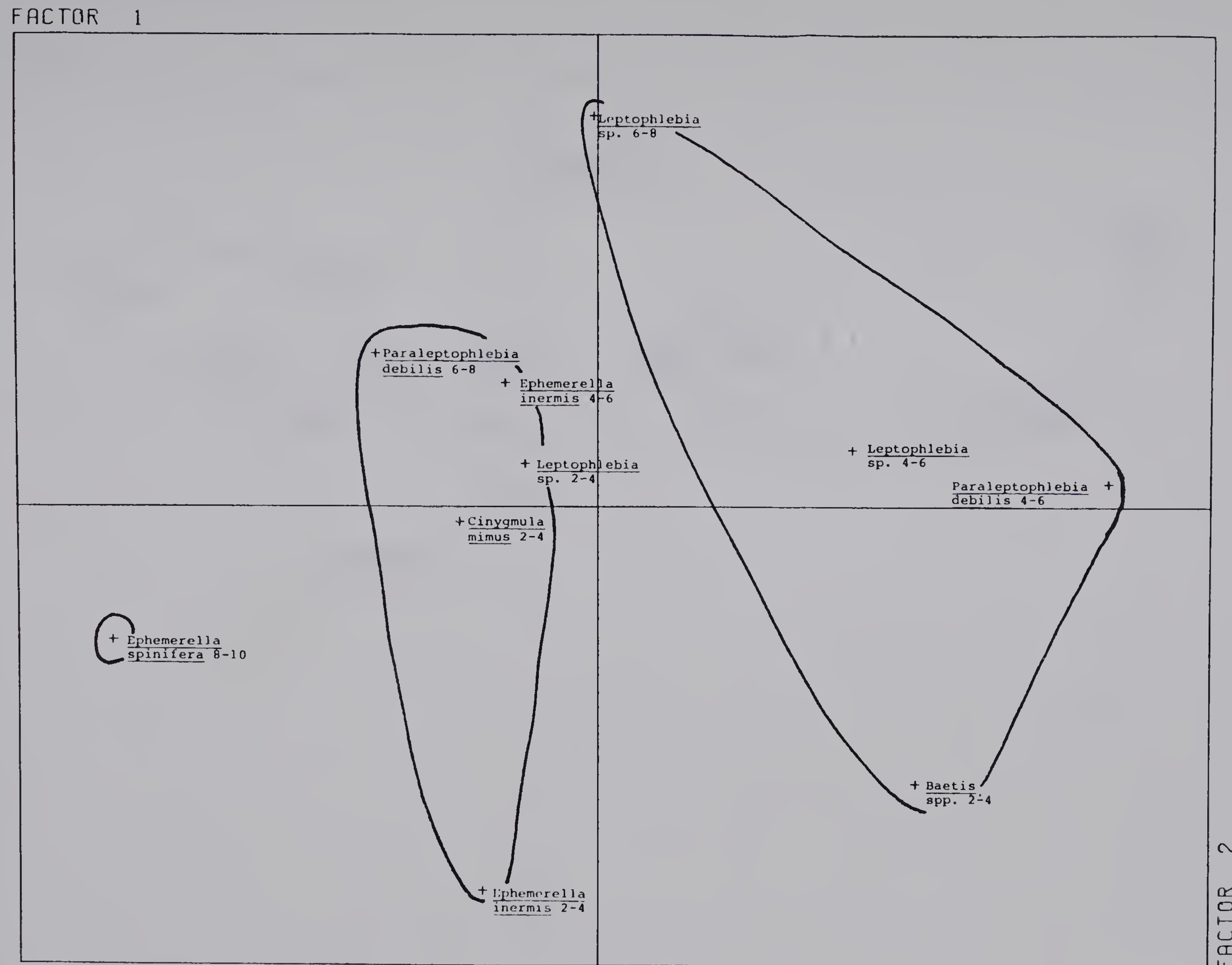
G. Stauffer 1, 14 February 1975



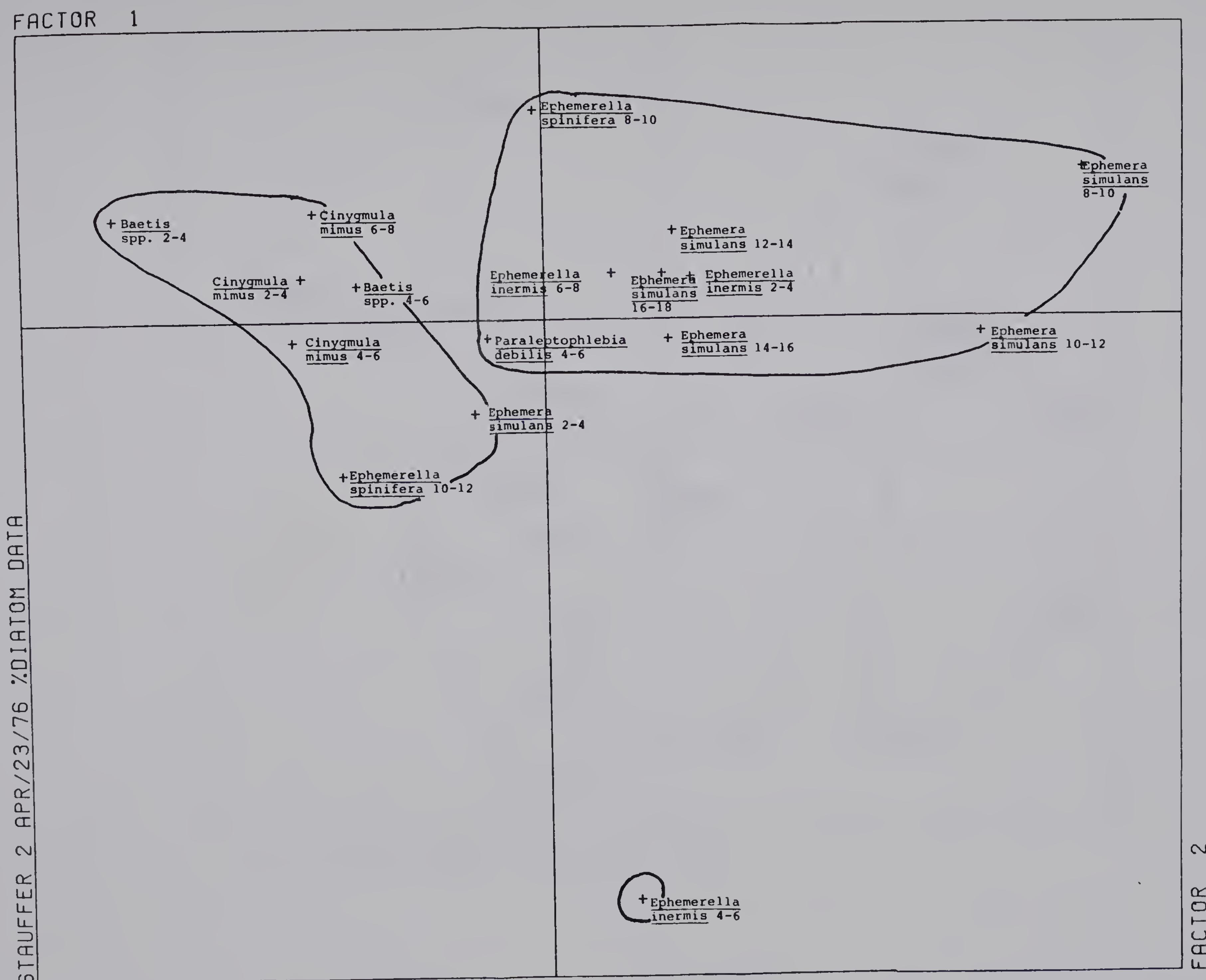
H. Stauffer 1, 23 April 1976



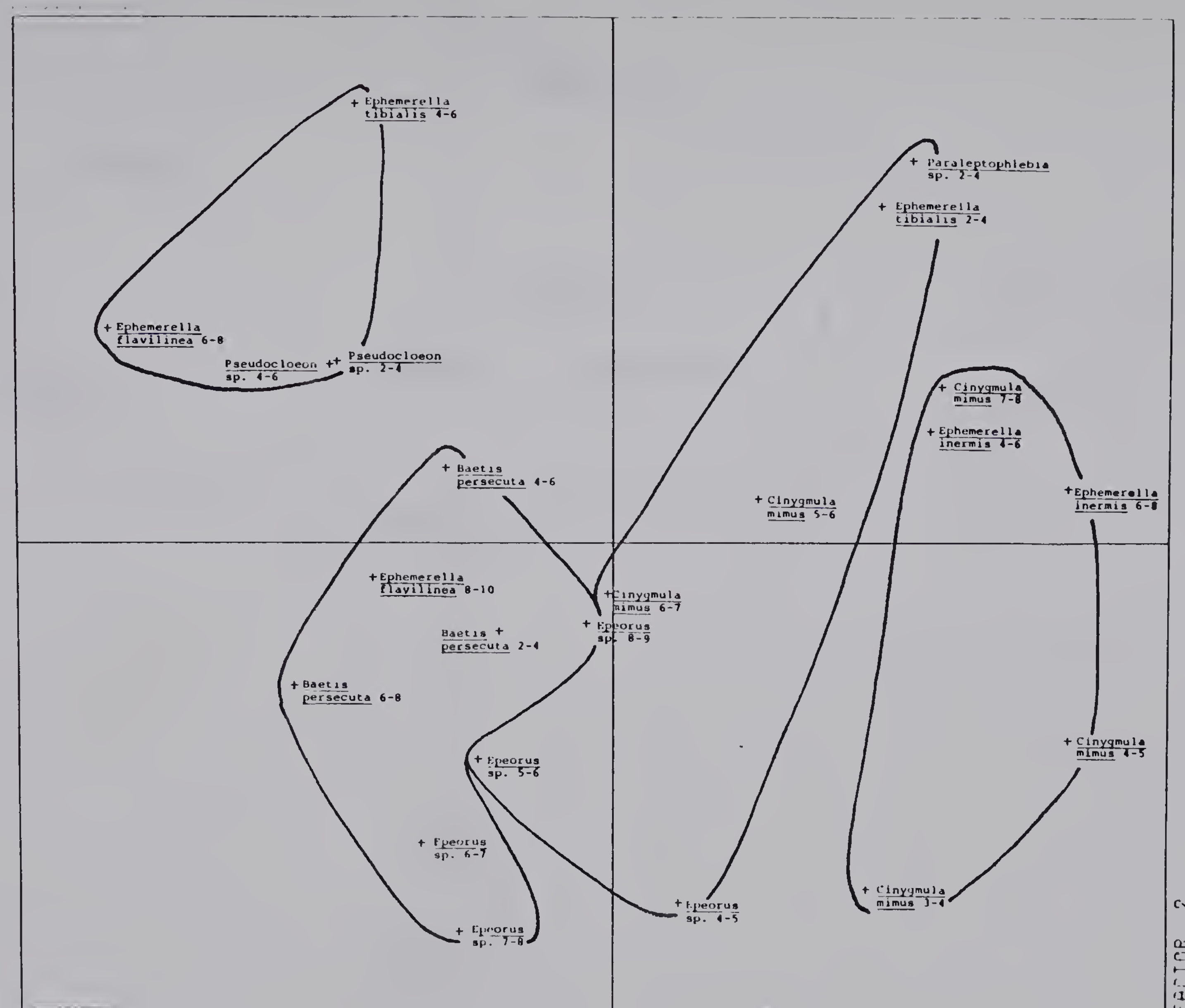
I. Stauffer 2, 18 October 1975



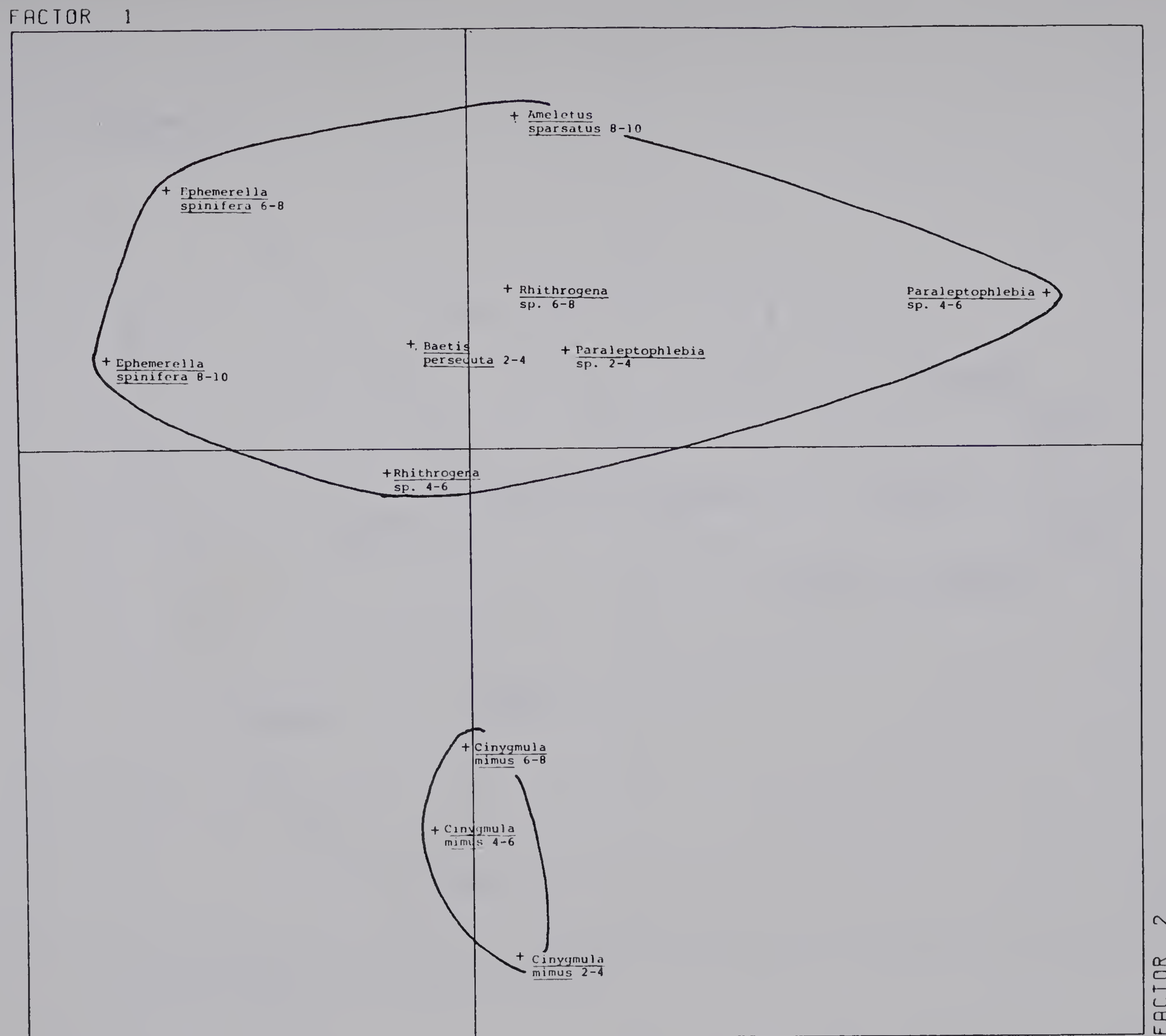
J. Stauffer 2, 14 February 1976



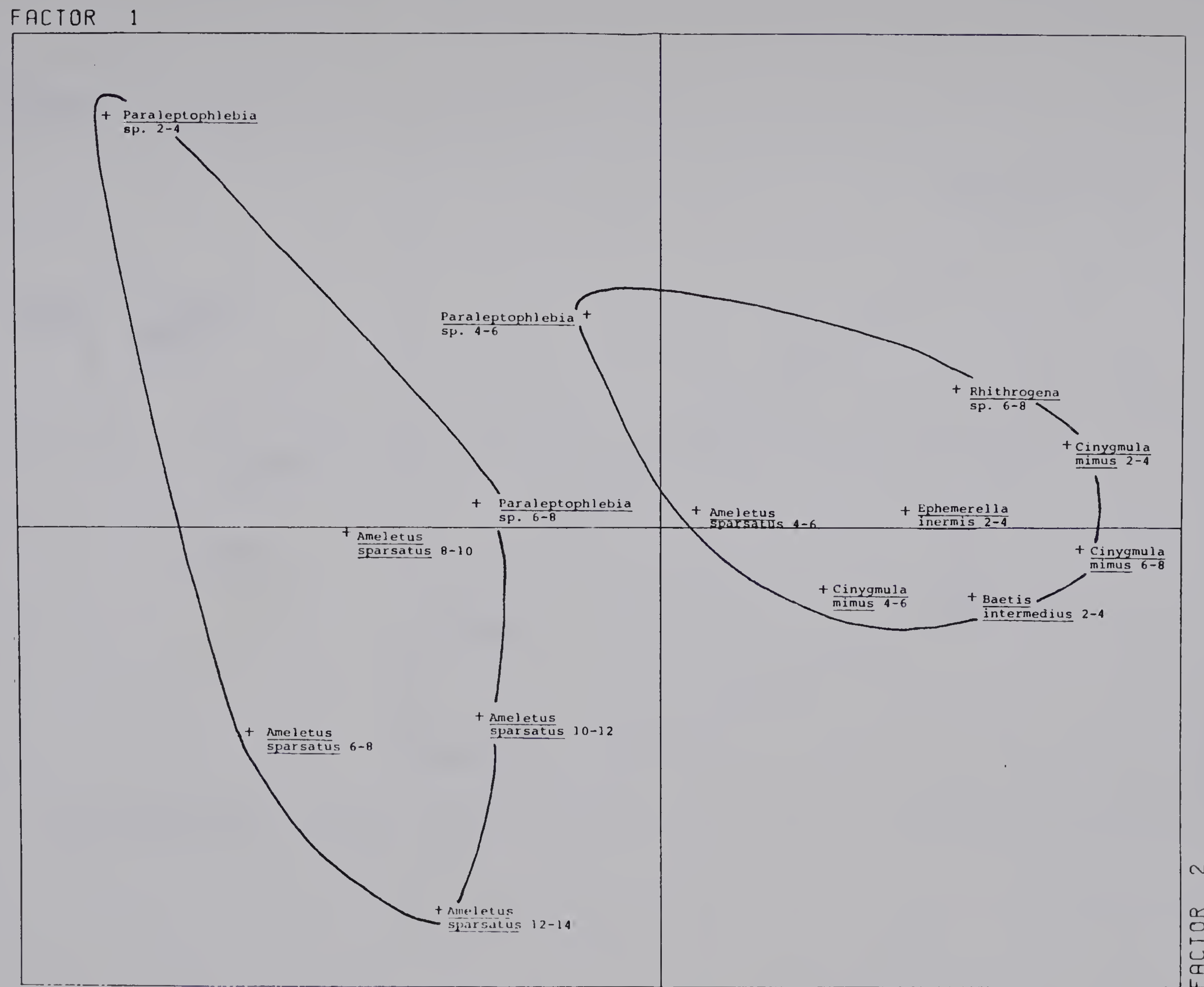
K. Stauffer 2, 23 April 1976



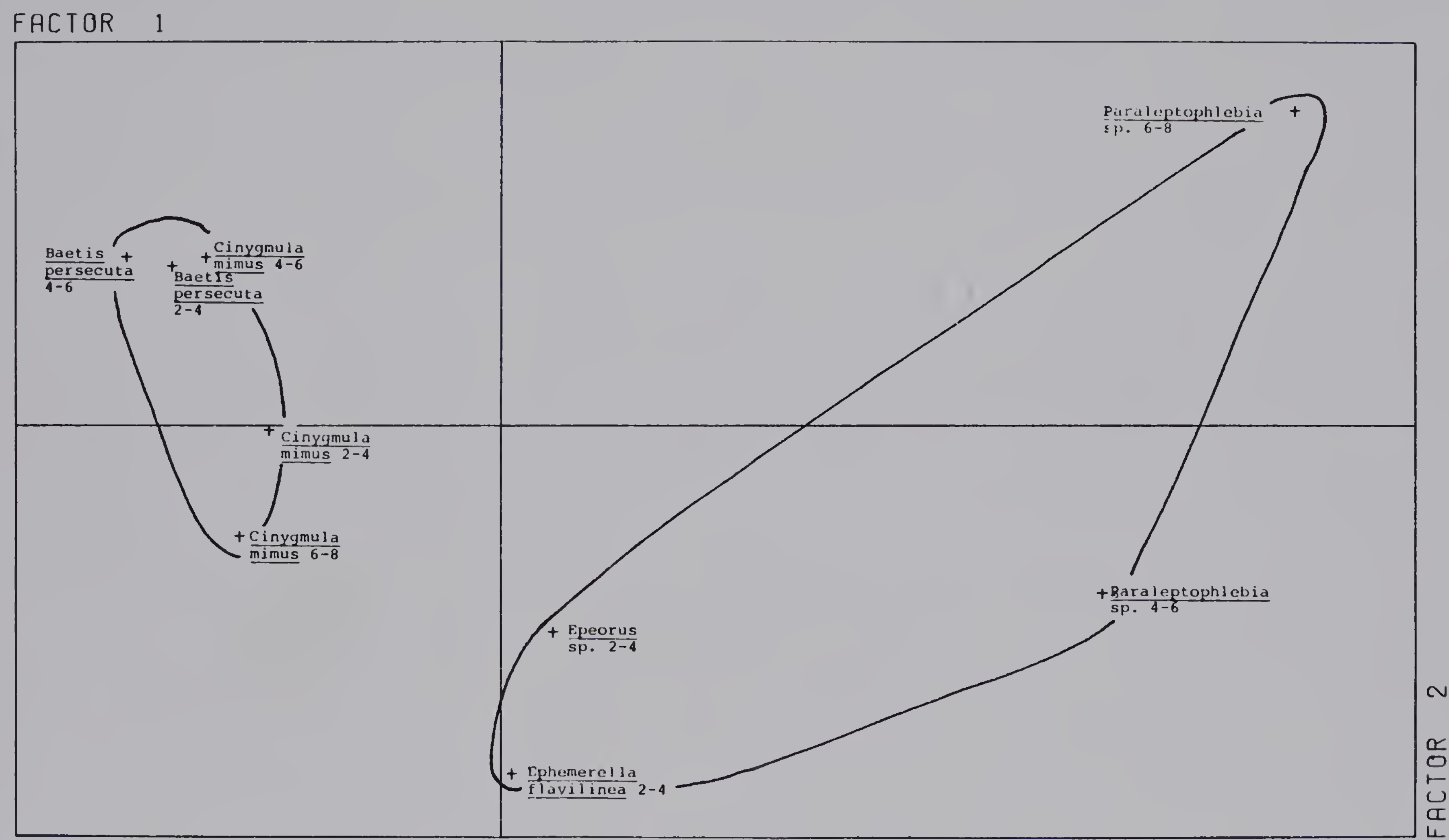
L. Tay River, 10 July 1975



M. Tay River, 14 November 1975



N. Tay River, 14 February 1976



O. Tay River, 13 May 1976